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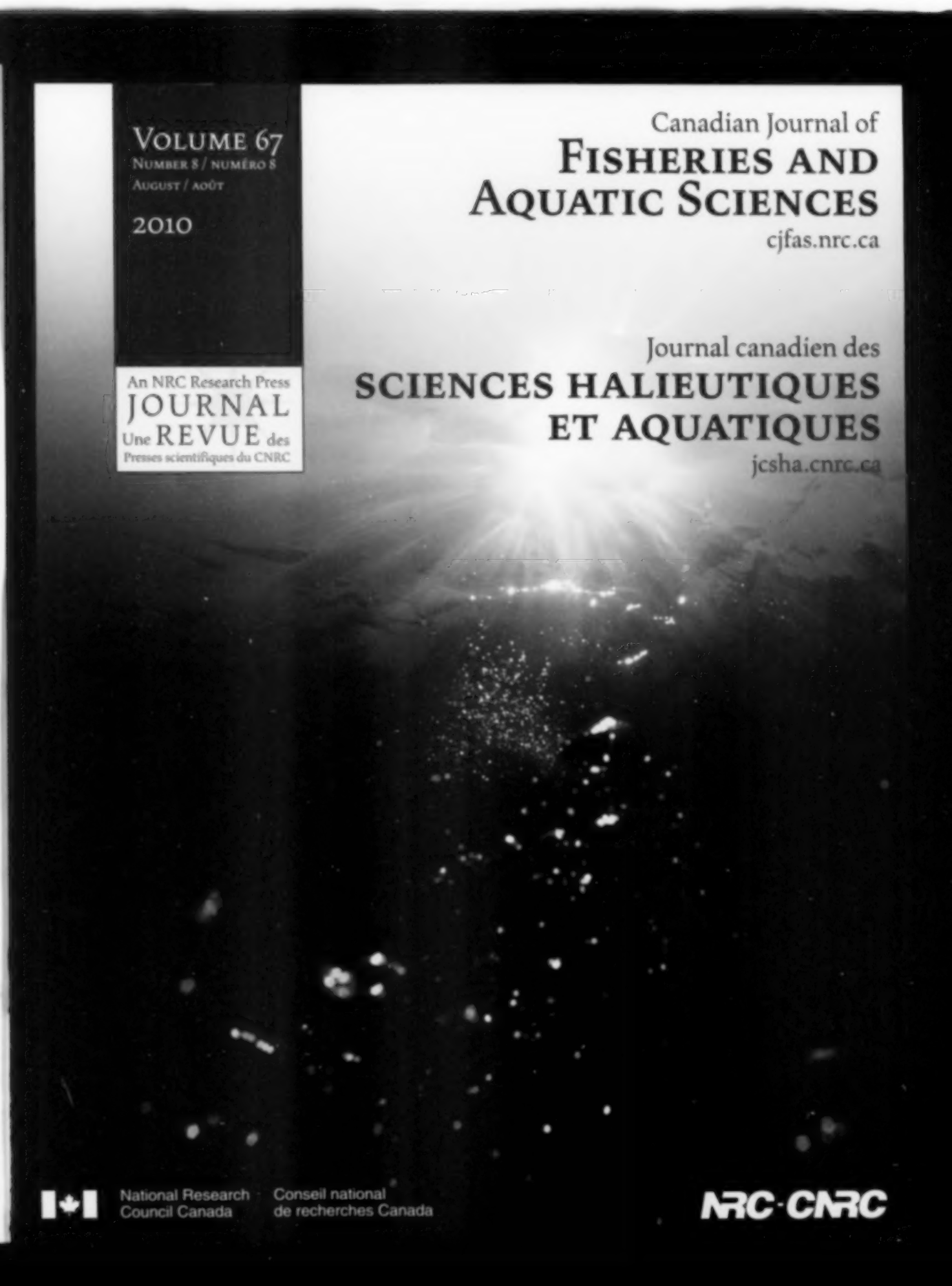

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RAPID COMMUNICATION / COMMUNICATION RAPIDE

Trends in the abundance of marine fishes

Jeffrey A. Hutchings, Cóilín Minto, Daniel Ricard, Julia K. Baum, and Olaf P. Jensen

Abstract: The Convention on Biological Diversity (CBD) established a target in 2002 to reduce the rate of biodiversity loss by 2010. Using a newly constructed global database for 207 populations (108 species), we examine whether the 2010 target has been met for marine fishes, while accounting for population biomass relative to maximum sustainable yield, B_{MSY}. Although rate of decline has eased for 59% of populations declining before 1992 (a pattern consistent with a literal interpretation of the target), the percentage of populations below B_{MSY} has remained unchanged and the rate of decline has increased among several top predators, many of which are below $0.5B_{MSY}$. Combining population trends, a global multispecies index indicates that marine fishes declined 38% between 1970 and 2007. The index has been below B_{MSY} since the mid-1980s and stable since the early 1990s. With the exception of High Seas pelagic fishes and demersal species in the Northeast Pacific and Australia–New Zealand, the multispecies indices are currently below B_{MSY} in many regions. We conclude that the 2010 CBD target represents a weak standard for recovering marine fish biodiversity and that meaningful progress will require population-specific recovery targets and associated time lines for achieving those targets.

Résumé : La Convention sur la diversité biologique (« CBD ») s'est donnée en 2002 comme objectif de réduire le taux de perte de la biodiversité avant 2010. Utilisant une nouvelle base de données globale de 207 populations (108 espèces), nous examinons si l'objectif 2010 de la CBD a été atteint pour les poissons marins, tout en tenant compte de la biomasse des populations relative au rendement maximal durable, B_{MSY}. Malgré une diminution du taux de déclin chez 59 % des populations en chute avant 1992 (une tendance qui correspond à une interprétation littérale de l'objectif 2010 de la CBD), le pourcentage des populations sous B_{MSY} s'est maintenu constant et le taux de déclin s'est accéléré chez plusieurs des prédateurs sommitaux, une majorité desquels sont à un niveau inférieur à $0.5B_{MSY}$. Combinant les tendances des populations, un indice global multi-espèces montre que les poissons marins ont diminué de 38 % entre 1970 et 2007. L'indice est inférieur à B_{MSY} depuis le milieu des années 1980 et stable depuis le début des années 1990. Avec l'exception des populations pélagiques de haute mer et des populations démersales du nord-est du Pacifique et de Nouvelle-Zélande–Australie, les indices multi-espèces sont présentement sous B_{MSY} dans plusieurs régions. Nous concluons que l'objectif CBD 2010 représente un faible standard pour récupérer la biodiversité des poissons marins et qu'un progrès réel requerra des cibles claires de récupération spécifiques à chacune des populations et soumises à des échéanciers stricts pour atteindre les objectifs visés.

Introduction

The United Nations declared 2010 to be the International Year of Biodiversity. This was a direct response to initiatives by the Convention on Biological Diversity (CBD) to (*i*) conserve biological diversity, (*ii*) use biological diversity in a sustainable fashion, and (*iii*) share the benefits of biological diversity fairly and equitably (CBD; http://www.cbd.int). In 2002, the Conference of the Parties adopted a strategic plan for the CBD, the mission statement of which articulated what has become known as the 2010 Biodiversity Target: "to achieve by 2010 a significant reduction of the current rate of biodiversity loss at the global, regional and national level as a contribution to poverty alleviation and to the benefit of all life on Earth" (http://cbd.int/2010-target/about.shtml).

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Among the biodiversity indicators identified by the CBD to evaluate progress in meeting the target are those that examine "trends in the abundance and distribution of selected species" and "trends in genetic diversity ... of fish species of major socio-economic importance". An intermediate and arguably more important metric of biodiversity is that of quantifying trends in the abundance of populations of selected species. This population-level approach, for example, underpins the only marine index formally under consideration by the CBD — the Marine Living Planet Index or MLPI (World Wildlife Fund for Nature (WWF) 2008). As Schindler et al. (2010) have shown recently, maintenance of population diversity can be of fundamental importance to the stability and persistence of species.

Our overall objective is to determine whether the CBD's 2010 target has been met for marine fishes. Our analysis represents a significant extension of the only global and regional examination of marine fish population trends (Hutchings and Baum 2005): trends are now considered for 207 populations (up from 177); the multispecies index includes 174 populations (up from 87); the most recent year included is now 2009 (compared with 2004); and the spatial scale has increased from one centred in the North Atlantic to one considerably more global in coverage.

Materials and methods

Our analyses utilize population biomass estimates compiled from assessments undertaken by national and international fisheries management agencies (soon to be available at www.marinebiodiversity.ca/RAMlegacy/srdb; detailed summaries of the data used in the present study are available upon request to J.A. Hutchings). Regionally, data were available from Northeast Atlantic (Iceland east to Baltic Sea), Northwest Atlantic (Canada, northeastern US), North Mid-Atlantic (southeastern US, Gulf of Mexico), Northeast Pacific (Bering Sea to southern California), Australia–New Zealand, High Seas (Atlantic, Pacific), and a limited number of populations from South Africa and South America.

Given that the 2010 target is based on the rate of change, we compared the slopes of linear regressions of log-transformed spawning stock biomass (SSB) against time for two different periods. For each population, we compared regression slopes for all available data up to 1991 (the year before the CBD was open for signature) with those for all available data from 1992 onwards (usually to 2007). The slopes for each population were estimated using the continuous piece-wise model:

$$(1) \qquad \ln(\mathrm{SSB}_t) = \alpha + \beta t + \delta_\beta (t - 1992)\eta_t + \varepsilon_t$$

where SSB_t is the spawning stock biomass (in tonnes) in year t, α is the overall intercept, η_t is a class variable determining whether year t is before ($\eta_t = 0$) or after ($\eta_t = 1$) 1992, β is the slope prior to 1992, δ_β is the change in slope post-1992, and $\varepsilon_t \sim \mathrm{N}(0, \sigma_\varepsilon^2)$ comprises the residuals. Under this model, a reduction in the rate of decline for those populations with negative slopes before 1992 would be reflected in a positive slope difference (i.e., $\delta_\beta > 0$), consistent with the 2010 target. Our analyses included populations (n = 207) for which there were at least 10 years of data before and after 1992 (Supplementary Table S1[1]). To examine the robustness of our results, we also fit a discontinuous piecewise model with no continuity constraint and a random-walk state–space model (Durbin and Koopman 2001) with pre- and post-1992 drift terms, using a Kalman filter (both are described in the Supplementary data[1]; all model fits and parameter estimates are shown in Supplementary Fig. S1 and Table S1[1]).

Potential consequences to biodiversity of positive and negative slope differences were evaluated by comparing each population's biomass (SSB or total biomass, TB) with the relevant estimated biomass at which maximum sustainable yield is achieved, i.e., $\mathrm{SSB}_{\mathrm{MSY}}$ or $\mathrm{TB}_{\mathrm{MSY}}$; for simplicity, we shall refer to these collectively as B_{MSY}. Following Worm et al. (2009), estimates of B_{MSY} available directly from stock assessments are based on SSB for all but two populations; these populations (North Atlantic albacore tuna, *Thunnus alalunga*; eastern Atlantic bluefin tuna, *Thunnus thynnus*) and those estimated from a Schaefer surplus production model, external to the stock assessments, are based on total biomass.

Multispecies abundance indices were constructed for 1970 (the initial year of WWF's MLPI) to 2007, using 174 populations in total (n = 159 having reference point estimates) for which data were available from at least 1978 until 2002 (ensuring a minimum of 25 years of data and at least 10 years of post-1992 data). To combine the series across populations, we standardized the SSB or TB data (depending on which reference point was available) by log-transforming and subtracting the biomass reference point on the log scale. For each year, the multispecies index was calculated using a mixed-effects model with a fixed-effect mean index per year, an overall random effect deviation for each population, and a first-order autocorrelation structure on the residuals. The trend was returned to the original scale by taking the exponent of the fixed-effect mean. The average of the first and last five years of this index were then used to calculate a percentage change across the 1970–2007 time period for all populations combined and for pelagic and demersal populations separately (habitat categories are indicated in Supplementary Table S1[1]).

Results

Temporal changes in rate of decline

Among 152 populations (73% of 207) declining prior to 1992, the slope difference was positive for 59% (n = 90; Fig. 1; four South African populations are not plotted), indicative of an easing of rates of decline after 1992. While 55 of these 90 populations showed an increasing trend after 1992, 35 of them were still declining, despite the positive slope difference. For the remaining 62 of 152 populations (41%), the rate of decline after 1992 was greater than that prior to 1992.

Information on B_{MSY} was available for 136 of the 152 populations in decline prior to 1992 (85 of which were obtained from assessments); the slope difference was positive for 62% of these, indicative of an easing of rates of decline after 1992. Among these 84 populations, 32 were still de-

[1] Supplementary data for this article are available on the journal Web site (http://cjfas.nrc.ca).

clining after 1992. For the remaining 52 of 136 populations (38%), the rate of decline increased after 1992.

Although rates of decline eased for more than half of marine fish populations globally, the proportional representation of populations above and below B_{MSY} did not change appreciably. For the 136 populations in decline prior to 1992, 84 were below B_{MSY} in 1992 (39 as estimated from assessments, 45 from surplus production models) compared with 81 at present (41 estimated from assessments and 40 from surplus production models). Among declining populations that were below B_{MSY} in 1992, the slope difference was positive for 58 of 84 (69%) after 1992.

To interpret temporal changes in slope difference within the context of potential reference points, we restrict regional descriptions to those populations for which estimates of B_{MSY} are available. (This data restriction has little effect on our results given the similarities in the proportional representation of populations experiencing various trends noted above and the minor reduction (n = 16) in populations considered.)

Regionally, the slope difference was positive for most populations in the Northwest Atlantic (78%), Northeast Atlantic (70%), and North Mid-Atlantic (90%), areas in which most populations were below B_{MSY} in 1992 and, on average, remain so today (Figs. 1*a*–1*c*). By comparison, the slope difference was positive for slightly less than half of the populations on the High Seas (45%), Australia – New Zealand (48%), and Northeast Pacific (45%) (Figs. 1*d*–1*f*), areas where most populations were larger than B_{MSY} in 1992.

For populations in decline prior to 1992 and that are still exhibiting a declining trend after 1992, despite a reduction in the rate of decline (n = 32), there were broad-scale regional differences in abundance relative to the MSY reference point. In the North Atlantic (Figs. 1*a*–1*c*), all 12 of these populations are below their reference targets and more than half (n = 7) are below $0.5B_{MSY}$. By contrast, among the remaining 19 populations (which are found in other regions), 14 are larger than B_{MSY} and only one (*Chrysophrys auratus*; New Zealand Area 8) is below $0.5B_{MSY}$ (Figs. 1*d*–1*f*). (Populations below $0.5B_{MSY}$ are defined as being overfished in the US and Australia (Hilborn and Stokes 2010).)

Most of the populations for which the rate of decline has increased since 1992 are top-level predators (maximum trophic level ≥ 4.3 for the 37 of 53 populations for which species-level diet data are available from www.fishbase.org), such as Atlantic cod (*Gadus morhua*), orange roughy (*Hoplostethus atlanticus*), and hoki (*Macruronus novaezelandiae*). Regionally, among the 15 North Atlantic populations declining more rapidly since 1992 (Figs. 1*a*–1*c*), 14 are below B_{MSY} and 12 are below $0.5B_{MSY}$. By comparison, few populations declining at faster rates elsewhere are below $0.5B_{MSY}$ (6 of 37 populations) and almost half (18 of 37) are above B_{MSY} (Figs. 1*d*–1*f*). Percentage changes were slightly higher when estimated by the discontinuous piecewise and random-walk models (Supplementary Table S1, Supplementary Figs. S1, S2)[3].

Multispecies indices of abundance

Overall, populations (n = 174) declined 38% between the first (1970–1974) and the last five years (2005–2009) in the time series. However, the index has stabilized since the early 1990s. The pattern of temporal change differed between pelagic and demersal fishes, which declined 28% and 41%, respectively.

Restricting the multispecies indices to the 159 populations for which estimates of B/B_{MSY} were available for the time period under consideration, populations declined 38% overall (from B/B_{MSY} = 1.28 to 0.79; Fig. 2*a*) and by 37% for pelagic (1.18 to 0.75) and 38% for demersal (1.30 to 0.80) populations (Fig. 2*b*). Regional B/B_{MSY} indices (Figs. 2*c*–2*h*) indicate that the steady decline in pelagic populations since the early 1970s, to levels below B_{MSY} beginning in the early 1990s (Fig. 2*b*), is evident in all regions except the North Mid-Atlantic (Fig. 2*e*). With the exception of High Seas populations (Fig. 2*h*), pelagic populations are, on average, below B_{MSY} on a regional basis.

Since declining from the early 1970s to the early mid-1990s, the demersal multispecies index has stabilized or possibly increased in recent years; demersal populations have been below B_{MSY} since the early 1980s (Fig. 2*b*). Comparing B/B_{MSY} in 2005–2009 with that from 1970–1974, demersal populations have declined 44% in the Northwest Atlantic (from B/B_{MSY} = 0.61 to 0.34), 46% in the Northeast Atlantic (0.88 to 0.47), 67% in the North Mid-Atlantic (1.40 to 0.47), and 59% in Australia – New Zealand (2.70 to 1.12). On average, demersal populations are below B_{MSY} in most regions except the Northeast Pacific and Australia – New Zealand.

Discussion

Interpreted literally, the CBD 2010 target might be said to have been met for marine fishes. Globally, rates of decline have eased for most (59%) populations declining prior to 1992. In three of six regions examined, rates of decline have eased for 63% or more of the populations. In the other regions examined, where rates of decline have eased for 45%–50% of populations, many declining populations (52 of 75) remain above B_{MSY} and would not normally be considered of conservation concern. In regions where populations are below B_{MSY}, multispecies trends in abundance appear to have stabilized in some areas and to be possibly increasing in others.

However, a strong argument can be made that a simple change in trends (which is what the 2010 target ultimately amounts to quantitatively) is insufficient as a metric for monitoring meaningful changes in biodiversity (Balmford et al. 2005; Hutchings and Baum 2005; Walpole et al. 2009). One obvious limitation is that it is not actually necessary for populations to be increasing in abundance for the target to be met; they simply need not be declining at a rate equal to or greater than what was experienced previously. Compounding this caveat is the observation that many populations remain low relative to their MSY reference points. For example, despite an easing of their rates of decline, all North Atlantic populations still decreasing after 1992 remain below B_{MSY} and more than half are below $0.5B_{MSY}$. Underscoring further the weak standard offered by the 2010 target are the observations that despite a reduction in rate of loss by 59% of marine fish populations, (*i*) the percentage of populations below B_{MSY} has remained unchanged since 1992 and (*ii*) the rate of decline has increased for 41% of populations, most of which comprise top predators and several of which (e.g., 80% of North Atlantic populations) are

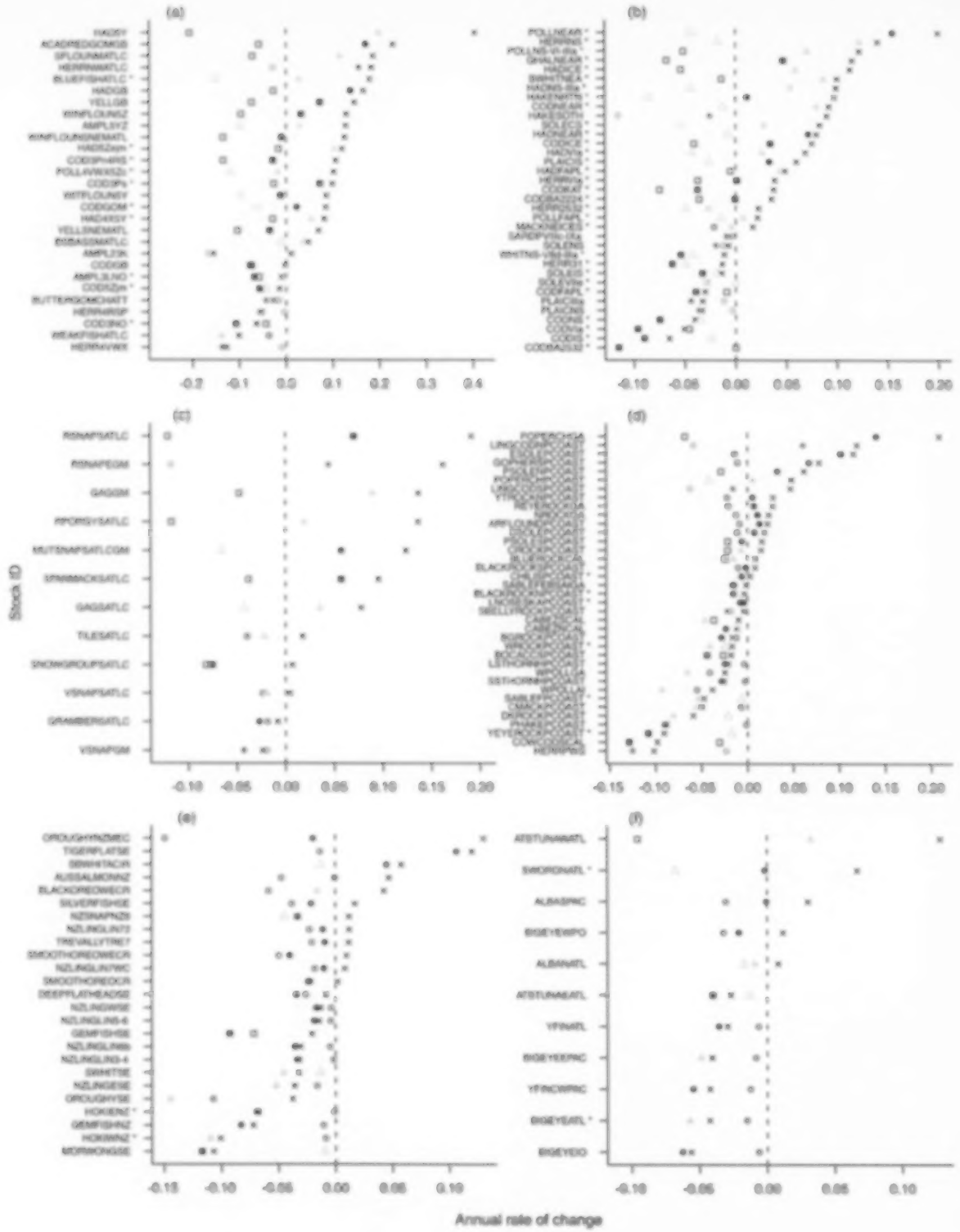
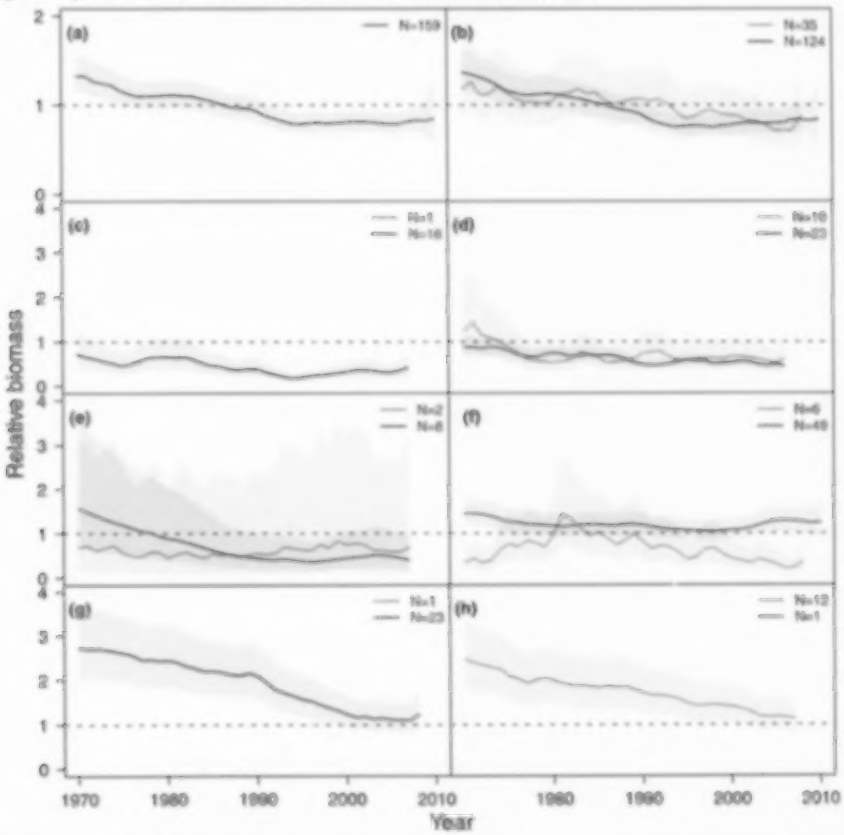

(a)
(b)
(c)
(d)
(e)
(f)
Stock ID
Annual rate of change

Fig. 1. Estimates of pre- and post-1992 slopes of the temporal trends (i.e., annual rate of change) of spawning stock biomass, log(SSB), for marine fish populations estimated to have been in decline prior to 1992. Descriptions of stock alphanumeric identification codes are given in Supplementary Table S1.[3] Data are plotted for populations in six regions: (*a*) Northwest Atlantic (n = 28); (*b*) Northeast Atlantic (n = 35); (*c*) North Mid-Atlantic (n = 12); (*d*) Northeast Pacific (n = 37); (*e*) Australia and New Zealand (n = 25); and (*f*) High Seas (n = 11). Within each region, populations are ordered by the difference in slope before and after 1992, indicated by an "×". Open symbols represent the temporal slope prior to 1992; solid symbols represent the temporal slope after 1992. Estimates of B_{MSY} obtained from stock assessments are indicated by an asterisk adjacent to the population name on the vertical axis of each panel; estimates of B_{MSY} for those without asterisks were obtained from a Schaefer surplus production model. Colours and shapes are used to categorize the 1992 and current size of each population relative to their MSY reference points: populations greater than B_{MSY} are green and are indicated by circles; those below B_{MSY} but greater than $0.5B_{MSY}$ are orange and are indicated by triangles; and those below $0.5B_{MSY}$ are red and are indicated by squares. Populations for which estimates of B_{MSY} are unavailable are indicated as shaded circles.

Fig. 2. Temporal trends in current biomass (B) relative to the estimated biomass at which the maximum sustainable yield should be obtained (B_{MSY}). B_{MSY} is set to 1 in each panel (broken lines). Multispecies index for all populations and regions combined is shown in (*a*). Remaining panels illustrate multispecies indices for pelagic (red) and demersal (green) populations separately (trend data for single populations within regions are not shown). Data for all regions by habitat type are shown in (*b*). Data are plotted separately for populations in six regions: (*c*) Northwest Atlantic; (*d*) Northeast Atlantic; (*e*) North Mid-Atlantic; (*f*) Northeast Pacific; (*g*) Australia and New Zealand; and (*h*) High Seas. The solid lines represent the fixed-effect mean yearly estimates, based on a mixed-effects model with population as a random effect. The shaded regions represent the 95% confidence intervals on the fixed-effect mean.



below $0.5B_{MSY}$. Even in regions dominated by populations larger than their single-species based estimates of B_{MSY} (e.g., Australia, Northeast Pacific), increased rates of decline by top predators may be of biodiversity concern within a multispecies, ecosystem context.

Since 1970, we estimate marine fish abundance to have decreased 38% globally (38% also for populations with estimates of B_{MSY}), a pattern that could be interpreted as being inconsistent with attempts to reduce biodiversity loss. The decline in the multispecies index reported here exceeds the 11% reduction in cumulative biomass since 1977 estimated by Worm et al. (2009), in part because trends in the latter were dominated by few large populations, whereas the multispecies index used here weighted each population equally. The decline that we report for marine fishes is more than double the 14% reduction of the MLPI between 1970 and 2005 (WWF 2008). Given that the MLPI includes abundance trends for multiple marine taxa (148 fish, 137 birds,

49 mammals, 7 reptiles), one possible explanation for our result is that marine fishes have been declining at a faster rate than other marine species.

One potential strength of our analysis is that it is limited to data obtained from models prepared and peer-reviewed by fisheries stock assessment scientists. We elected not to include trend data based solely on survey and fishery catch rates because of unestimated temporal and spatial biases that can exist in these data. However, by excluding catch and catch-rate data, we have also excluded data-poor species from areas where severe depletions are thought to have occurred (e.g., west Africa, southeast Asia), noncommercial species, and many species of conservation concern. For example, of the 38 marine fishes assessed as being endangered, threatened, or of special concern in Canadian waters (www.cosewic.gc.ca; accessed 4 June 2010), only eight are represented here. Our strict criterion also resulted in the exclusion of all but one chondrichthyan, a class of fishes considered to be at heightened risk of extinction worldwide (Baum et al. 2003; Dulvy and Forrest 2010). Our findings should also be tempered by the fact that many species whose catches (direct and incidental) are illegal or unreported have not been included.

It is difficult to judge precisely how the inclusion of these species might have influenced our results. On the one hand, their inclusion might have increased the percentage of populations meeting the 2010 target. Of Hutchings and Baum's (2005) 54 data sets that were based solely on catch rates, 76% showed a positive slope difference, which might partially account for the considerably higher percentage of populations (81%) that they reported as having a positive slope difference since 1992. On the other hand, because of their generally higher pre-1992 slopes and higher post-1992 slope differences, inclusion of these populations may have had the effect of accentuating some declines or of dampening some increases in multispecies indices of abundance.

The present work represents a significant expansion of data considered in the only previous analysis of changes in the rate of decline of marine fishes (Hutchings and Baum 2005). Most populations assessed by national and international agencies were declining before 1992. Since then, the rate of decline has been reduced in 59% of populations, a pattern consistent with the 2010 CBD target. For the remaining 41% of populations, most of which comprise top predators, the rate of decline has increased; most of those in the North Atlantic remain below $0.5B_{MSY}$, whereas the majority of those elsewhere are above their MSY reference target. Although declining trends have been reversed in many populations, meaningful progress in recovering marine fish biodiversity will almost certainly involve the establishment of specific recovery targets and specific time lines to achieve those targets (Hutchings and Baum 2005; Shelton and Sinclair 2008).

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Nutrient loading by anadromous alewife (*Alosa pseudoharengus*): contemporary patterns and predictions for restoration efforts

Derek C. West, Annika W. Walters, Stephen Gephard, and David M. Post

Abstract: Anadromous alewives (*Alosa pseudoharengus*) have the potential to alter the nutrient budgets of coastal lakes as they migrate into freshwater as adults and to sea as juveniles. Alewife runs are generally a source of nutrients to the freshwater lakes in which they spawn, but juveniles may export more nutrients than adults import in newly restored populations. A healthy run of alewives in Connecticut imports substantial quantities of phosphorus; mortality of alewives contributes 0.68 g P·fish^{-1}, while surviving fish add 0.18 g P, 67% of which is excretion. Currently, alewives contribute 23% of the annual phosphorus load to Bride Lake, but this input was much greater historically, with larger runs of bigger fish contributing 2.5 times more phosphorus in the 1960s. A mesocosm experiment in a nearby lake showed that juvenile alewife growth is strongly density dependent, but early survival may be too low for juvenile outmigration to balance adult inputs. In eutrophic systems where nutrients are a concern, managers can limit nutrient loading by capping adult returns at a level where juvenile populations would not be suppressed.

Résumé : Les gaspareaux (*Alosa pseudoharengus*) anadromes peuvent potentiellement modifier les bilans de nutriments des lacs côtiers pendant leurs migrations adultes vers les eaux douces et leurs migrations juvéniles vers la mer. Les montaisons de gaspareaux sont généralement des sources de nutriments pour les lacs d'eau douce dans lesquels ils fraient, mais, dans les populations nouvellement rétablies, les jeunes peuvent exporter plus de nutriments que les adultes n'en importent. Une montaison saine au Connecticut importe des quantités importantes de phosphore; la mortalité des gaspareaux fournit 0,68 g P·poisson^{-1}, alors que les poissons survivants apportent 0,18 g P, dont 67 % est de l'excrétion. Actuellement, les gaspareaux fournissent 23 % de la charge annuelle de phosphore du lac Bride, mais cet apport était beaucoup plus élevé dans le passé lorsque, durant les années 1960, des montaisons plus importantes de poissons plus grands fournissaient 2,5 fois plus de phosphore. Une expérience en mésocosme dans un lac adjacent montre que la croissance des gaspareaux est fortement reliée à la densité, mais que la survie au début du cycle est peut-être trop faible pour que l'émigration des jeunes contrebalance les apports des adultes. Dans les systèmes eutrophes dans lesquels les gestionnaires se préoccupent des nutriments, ceux-ci peuvent contrôler la charge de nutriments en limitant les retours d'adultes au niveau nécessaire pour que les populations de jeunes ne soient pas réduites.

[Traduit par la Rédaction]

Introduction

In coastal watersheds across New England, diadromous fish are regaining access to inland waters from which they have been barred for a century or more. The removal of dams and the installation of fishways have already reopened 250 miles of stream to diadromous fish in the state of Connecticut, USA alone. Restoration of the spatial connection between the ocean and freshwater ecosystems is a priority for diadromous fish management and conservation (Atlantic States Marine Fisheries Commission 2009). Diadromous fish are essential components of both the freshwater and marine systems in which they reside; however, many diadromous fish species are in decline (Limburg and Waldman 2009). While species such as Atlantic salmon (*Salmo salar*) and American shad (*Alosa sapidissima*) have garnered the preponderance of public attention, ecological interactions may be most strongly influenced by less glamorous, but historically more abundant fish such as alewife (*Alosa pseudoharengus*), and blueback herring (*Alosa aestivalis*) (collectively called river herring).

Alewives are an important component of the marine and

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freshwater ecosystems in which they reside. Juvenile alewives are extremely effective size-selective predators, driving strong changes in zooplankton community structure and causing trophic cascades in their natal rearing lakes (Brooks and Dodson 1965; Post et al. 2008). Juvenile alewives are important prey for largemouth bass (*Micropterus salmoides*) and pickerel (*Esox* spp.) (Cooper 1961; Yako et al. 2000) and adults are important prey for costal predators and piscivorous birds (Hartman 2003; Dalton et al. 2009). In the fall, juvenile anadromous alewives migrate to the ocean where they feed and grow for several years before returning to their natal systems to spawn. Although the migration of adult alewives is obstructed by even low-head dams, they will readily ascend fishways, making them a good target for restoration efforts (Havey 1961).

One consequence of reconnecting freshwater ecosystems to the coastal ocean is the reestablishment of the movement of nutrients by diadromous fish between the ocean and inland waters. While an enormous amount of research has focused on the role of Pacific salmon in loading marine-derived nutrients into freshwater ecosystems (Donaldson 1969; Bilby et al. 1996; Naiman et al. 2002), much less is known about the role of other anadromous fish as nutrient vectors, particularly those in the Atlantic Ocean. Like Atlantic salmon, alewives are iteroparous, with about half of adults surviving spawning to return to sea (Cooper 1961; Kissil 1974; Dalton et al. 2009). Inputs from carcasses, gametes, and excretion make anadromous alewives a potentially sizable source of marine-derived nutrients for the streams through which they migrate (Post and Walters 2009; Walters et al. 2009) and lakes in which they spawn. Marine-derived organic matter from alewives has been shown to be incorporated into stream invertebrates and piscivores (Garman and Macko 1998; Walters et al. 2009). The one available estimate of nutrient loading to lakes suggests that anadromous alewives may contribute considerably more nitrogen and phosphorus to freshwater ecosystems, on an areal basis, than many Pacific salmon runs (Durbin et al. 1979).

Alewife populations have changed considerably since the 1970s when Durbin et al. (1979) studied the movement of nutrients by alewives. Despite restoration efforts, alewife populations are in decline throughout much of their native range (Atlantic States Marine Fisheries Commission 2009; Limburg and Waldman 2009). Dramatic declines have been seen from 1950 to 2000 in both commercial fisheries landings and the passage of river herring through monitoring stations on fish passes (Davis and Schultz 2009). In addition to the decline in population size, the body size of alewife spawners has decreased substantially. Historically, the alewife run at Bride Lake, Connecticut, consisted of fish that were age 5 or greater, but currently, the run is dominated by smaller age 3 and 4 fish (Davis and Schultz 2009).

While Pacific salmon typically spawn in nutrient-poor lakes and streams where marine-derived nutrients are considered ecologically beneficial (Stockner 1987; Gresh et al. 2000; Naiman et al. 2002), alewives transport nutrients into and out of freshwater ecosystems that are typically quite productive. Coastal ecosystems throughout southern New England are naturally mesotrophic and are typically imbedded within a human-dominated landscape where cultural eutrophication is a persistent management concern (Brugam 1978). In this context, the restoration of anadromous alewives could exacerbate water quality problems if alewives increase net nutrient loading into the freshwater ecosystems where they spawn. This has caused concern among some local stakeholders and has the potential to delay or prevent restoration efforts in watersheds where nutrient loading is a primary water quality concern (e.g., where the US Environmental Protection Agency has mandated Total Maximum Daily Load studies for nutrient abatement).

Anadromous fish move nutrients both into and out of freshwater ecosystems, although inputs are typically more obvious and much better studied (Moore and Schindler 2004). Net loading into freshwater ecosystems is fully described as inputs due to adult mortality, gametes, and direct excretion of nutrients minus the removal of nutrients from freshwater ecosystems by juvenile fish when they emigrate. Since juvenile growth and survival in freshwater are typically density dependent (Jonsson et al. 1998), anadromous fish can export nutrients from freshwater ecosystems when at low densities and import nutrients when at high densities (Scheuerell et al. 2005). This sets up the potential for anadromous alewives to export nutrients from freshwater ecosystems early in restoration when adult densities are low and to import large quantities of nutrients as adult returns (escapement) increase.

Here, we evaluate the patterns of net nutrient loading by alewives over a range of population sizes. We concentrate on phosphorus, as it is generally the nutrient that limits production in the lake ecosystems in which alewives spawn (Schindler 1978). First, we estimate net alewife nutrient loading and parameterize an alewife nutrient loading model using data from an existing run of anadromous alewives in Bride Lake. We then compare the current alewife nutrient load to that in the 1960s when alewives were more numerous and larger. Next, since little is known about the actual patterns of nutrient loading during restoration, we predict the net nutrient loading for a newly restored population across a range of adult escapement. We use a local sensitivity analysis to determine which parameters are most important to the alewife nutrient loading model. Finally, we use an export coefficient model to estimate the landscape phosphorus loading to Bride Lake and Linsley Pond to place the alewife loading term in the context of the lake's nutrient budget.

Materials and methods

Study site

Our research was conducted at Bride Lake and Linsley Pond in Connecticut. Bride Lake contains an anadromous alewife population that we used to both evaluate contemporary and historic net nutrient loading by an alewife population and parameterize our general alewife nutrient loading model. Bride Lake is the site of extensive historical (Marcy 1969; Kissil 1974) and current research on alewife (Davis and Schultz 2009; Post and Walters 2009). It is located in East Lyme, Connecticut, and is linked to Long Island Sound by Bride Brook, which flows 3.3 km from the outlet of Bride Lake to Long Island Sound (see Dalton et al. 2009 for map). Bride Lake is 28.7 ha in area (based on a high-resolution areal photograph, not 18 ha, as previously reported

in Kissil (1974)), has a maximum depth of 10.7 m (Kissil 1974), and had an average summer total phosphorus (TP) concentration of 21.3 μg P·L^{-1} from 2005 to 2007. The Bride Lake anadromous alewife population was studied in the 1960s by Kissil (1974) to evaluate characteristics of the spawning population and young-of-the-year (YOY) in the lake. Since 2003, the Connecticut Department of Environmental Protection (CTDEP) has monitored the number of adults returning to Bride Lake to spawn using a blocking weir (2003–2005; Davis and Schultz 2009) and a Smith-Root SR-1601 fish counter (2005–2008). In 2005, the fish counter was also used to estimate the number of adults leaving Bride Lake. YOY alewives in Bride Lake were sampled monthly from June to August from 2004 to 2006 in a pelagic purse seine with 3.18 mm mesh. The seine was 4.87 m deep and 35.45 m long and encircles an area of 100 m^2.

Linsley Pond is a 9.4 ha pond with a maximum depth of 13.4 m located on the border of Branford and North Branford, Connecticut. Linsley Pond flows into Pisgah Brook, which runs 3.9 km to the Branford Supply Ponds Dam and then another 1.6 km to Branford Harbor and Long Island Sound. The river linkage between Linsley Pond and Long Island Sound was severed in 1900 by the construction of the Branford Supply Ponds Dam. A fishway was built at the Branford Supply Ponds Dam in the fall of 2005. In the first year that the fishway was opened, 3123 adult alewives entered the supply ponds, and although no alewives have been confirmed in Linsley Pond to date, they are expected to reach Linsley Pond in the coming years. Excessive nutrient inputs from development and industry have led the CTDEP to develop a Total Maximum Daily Load for the watershed in 2005. The analysis found that Linsley Pond currently receives ~100 kg P annually and recommended a 43% reduction in TP inputs. In 2005, the lake had a spring TP concentration of 150 μg P·L^{-1}.

Alewife nutrient loading model

Here, we present a fully described nutrient loading model for anadromous fish. With an annual time step, the general model estimates net phosphorus flux from alewives as

$$\text{Net P flux} = n_a \times (P_{mort} + P_{gametes} + P_{excretion}) - P_{YOY}$$

where n_a is the number of adults, P_{mort} is the phosphorus loaded into the lake by adult mortality, $P_{gametes}$ is the phosphorus loaded into the lake by inputs of eggs and sperm, and $P_{excretion}$ is the phosphorus loaded into the lake through direct excretion of phosphorus by adults during their residence in the freshwater ecosystem; P_{YOY} is export of phosphorus by YOY or juvenile fish as they emigrate from the ecosystem. The n_a was used as a dynamic variable to look at patterns of net nutrient loading across a range of adult densities.

The mass of phosphorus loaded per fish by adult mortality (P_{mort}) was modeled as

$$P_{mort} = \mu_a \times \text{mass}_a \times [P_a]$$

where μ_a is the adult in-lake mortality rate (per year), mass_a is the average mass of the adults (wet weight) entering the lake, and $[P_a]$ is the concentration of phosphorus in adults (grams phosphorus per gram wet weight). We used counts of adult immigration and emigration taken at the Bride Lake outlet in 1966 and 1967 by Kissil (1974) and in 2005 by the CTDEP to estimate μ_a. Current mass_a was estimated directly from 120 sampled fish entering Bride Lake in 2004, 2005, and 2008. The mass_a from the 1960s was determined using the length of fish found by Kissil (1969) and the length–weight regression for current adult alewives in Bride Lake. The phosphorus content of unspawned adults ($[P_a]$) was taken from Durbin et al. (1979).

The mass of phosphorus loaded per fish by gametes ($P_{gametes}$) was modeled as

$$P_{gametes} = (1 - \mu_a) \times 0.5 \times (F_a \times \text{mass}_e \times [P_e] + \Delta\text{mass}_t \times [P_t])$$

where F_a is the fecundity of each female, mass_e is the mass of each egg, $[P_e]$ is the concentration of phosphorus in each egg (grams phosphorus per gram wet weight), Δmass_t is the change in mass of the testes, and $[P_t]$ is the concentration of P in the testes. The ovaries of 10 anadromous alewives taken at the entrance of Bride Lake in early May of 2004 and April of 2005 were measured for mass_e and $[P_e]$. The F_a was estimated as a function of adult length (length_a) based on the relationship $F_a = 3596\ (\text{mm}^{-1}) \times \text{length}_a - 766186$ ($n = 24$, $t = 4.04$, $r^2 = 0.43$, $p < 0.01$) derived from data in Kissil (1969) and from fish sampled in 2004 and 2005. The change in mass of the testes was calculated as the mass of the testes of unspawned alewives minus the mass of the testes of spawned fish. The initial mass of testes was estimated as a function of length_a and based on the relationship $\text{mass}_t = 0.157\ (\text{g·mm}^{-1}) \times \text{length}_a - 28.563$ ($n = 289$, $t = 13.64$, $r^2 = 0.39$, $p < 0.01$) for fish captured at the entrance to Bride Lake in 2003 and 2006 (J.P. Davis, CTDEP Inland Fisheries Division, Eastern District Headquarters, 209 Hebron Road, Marlborough, CT 06447, USA, unpublished data). The mass of spawned testes was taken to be 5.18 g (Durbin et al. 1979). The $1 - \mu_a$ term was included because we assume that all of the phosphorus contained in a fish remains in the lake when that fish dies. Thus, P_{mort} includes $P_{gametes}$ for each adult that dies and the $1 - \mu_a$ term was included to avoid double counting $P_{gametes}$ from adults that die. We assumed a 1:1 sex ratio.

The mass of phosphorus loaded through direct excretion ($P_{excretion}$) was modeled as

$$P_{excretion} = (1 - \mu_a) \times \text{mass}_a \times E_a \times t_a$$

where E_a is the excretion rate of adults (grams phosphorus per gram wet weight per day) and t_a is the time spent in freshwater by spawning adults. Again, the $1 - \mu_a$ term was included because we assume that fish that die contribute all of their phosphorus to the lake. Excretion is only accounted for in fish that survive spawning and leave the system. The time that adult alewives spend in freshwater was set as 14 days, which corresponds to the median stay in freshwater for alewives at the time when migration peaks (Kissil 1969). Adults do not feed between migration and spawning, so all nutrients excreted during this time are of marine origin (Cooper 1961). Adults may feed in the lake between spawning and returning to the ocean but this time is generally short. The E_a was calculated with alewives entering Bride Lake (Post and Walters 2009).

The mass of phosphorus exported from the lake by YOY alewives (P_{YOY}) was modeled as

$$P_{YOY} = n_{YOY} \times mass_{YOY} \times [P_{YOY}] \times area$$

where $n_{YOY} \times mass_{YOY}$ is a density-dependent function that relates the biomass density of YOY alewives to the number of adult spawners, $[P_{YOY}]$ is the concentration of phosphorus in each YOY alewife (grams phosphorus per gram wet weight), and area is the lake area in hectares. The biomass density of YOY alewives ($n_{YOY} \times mass_{YOY}$) emigrating from the lake was calculated on an areal basis and was modeled as a function with an exponential rise-to-maximum as the number of YOY individuals increases. The form of $n_{YOY} \times mass_{YOY}$ was estimated from the mesocosm experiment performed in Linsley Pond in the summer of 2005 (see below). This density-dependent relationship reflects a decrease in growth and survival as the number of juveniles increases. The $[P_{YOY}]$ was measured in 13 YOY alewives caught in Bride Lake in the falls of 2004 and 2005.

Density-dependent growth and survival of YOY alewives

In the summer of 2005, we conducted a mesocosm experiment in Linsley Pond to estimate the density-dependent growth and survival of YOY alewives. Each mesocosm was 2 m in diameter with 6 m deep cylindrical sides of solid polyethylene. They were closed on the bottom and open to the atmosphere on top. Mesocosms were lowered to around 7 m depth and raised through the water column isolating approximately 19 m^3 of water from the lake. We stocked YOY anadromous alewives from Bride Lake into the mesocosms on 12 July 2005 at densities that spanned the range of densities observed in local lakes with anadromous alewives. We had one treatment with a density of 0.32 fish·m^{-2} (one fish per mesocosm) replicated three times. The other five treatments, with densities of 0.64, 1.27, 2.55, 5.1, and 10.19 fish·m^{-2} (2, 4, 8, 16, and 32 fish per mesocosm), were replicated two times. Fish stocked into mesocosms had an average length of 32 mm (SD = 3.1 mm) and an average mass of 0.26 g (SD = 0.09 g). Fish were stocked at this size because fish <25–30 mm are difficult to keep alive during transport. Nitrogen and phosphorus were added to each mesocosm at a 25:1 molar ratio based on a phosphorus loading rate of 0.30 mg P·m^{-3}·day^{-1}. The sides of the mesocosms were scrubbed clean of periphyton weekly. Fish were censused on 26 July and 16 August and a final count was made on 30 August when all fish were removed from the mesocosms to be measured for length and mass. One of the 0.32 fish·m^{-2} treatments was omitted due to the inadvertent addition of a fish in the middle of the experiment.

We fit a negative exponential model to the growth rate of YOY alewives across stocking densities and a linear model to mortality rate across stocking densities. The relationship between initial fish density and final biomass density of YOY produced was fit with an asymptotic exponential function:

$$n_{YOY} \times mass_{YOY} = a \times (1 - e^{-b \times x})$$

where $n_{YOY} \times mass_{YOY}$ is the biomass density (grams per square metre) of YOY alewives, a is the maximum biomass density (asymptote), b is the slope of the relationship between density and biomass, and x is the initial density of YOY alewives at stocking. Linsley Pond is more productive than Bride Lake, so we expected to obtain greater densities of YOY alewives in the Linsley Pond mesocosms than in Bride Lake. To translate the biomass from the experiment to biomass in Bride Lake, we matched a to the biomass density of YOY alewives observed in midsummer in Bride Lake for 2004 and 2005, which was 1.60 g·m^{-2} (Post et al. 2008). The year 2006 was excluded because an early emigration event of YOY alewives greatly reduced their midsummer density. The initial density x of YOY alewives was converted to the number of spawners (n_a) by fitting an exponential decline between the time when eggs were spawned on 1 May and 12 July, when fish were stocked into the mesocosms. Using the number of spawners and fecundity, we can estimate the number of eggs spawned and measure the slope of the exponential decline to the time at which we were first able to estimate the population size using a purse seine, which was 30 June in 2005 and 19 June in 2006.

The mesocosm experiment provides a good estimate of the density-dependent growth of alewives larger than 30 mm in Linsley Pond, but we do not know the growth or survival of smaller alewives. The survival of alewives in Bride Lake provides a best estimate of early survival; however, early survival is likely density dependent and survival could be considerably higher at densities lower than that seen in Bride Lake. Therefore, in the estimate of potential nutrient export from Linsley Pond, we also examine the case where the survival of YOY alewives to 30 mm increases 10-fold from that seen in Bride Lake.

Phosphorus content of fish (adults, gametes, and YOY)

Phosphorus content of unspawned adult alewives and alewife testes was taken from Durbin et al. (1979). Phosphorus content of eggs and YOY was estimated by ashing dried samples in a muffle furnace followed by digestion with HCl and analysis of liberated soluble reactive phosphorus on an Astoria 2 autoanalyzer (Higgins et al. 2006).

Sensitivity analysis

We conducted a local sensitivity analysis of our alewife nutrient loading model for the current alewife run in Bride Lake to determine the relative importance of each parameter to the estimation of net nutrient flux. The sensitivity measures the percent change in the model output for a 1% change in a parameter. We varied n_a, μ_a, $mass_a$, $[P_a]$, F_a, $mass_e$, $[P_e]$, $\Delta mass_y$, $[P_i]$, t_a, and E_a by sequentially adjusting each parameter by ±10% and recording the centered distance estimate of the response of the net nutrient flux:

$$s_i = \frac{Y(1.1 \times p_i) - Y(0.9 \times p_i)}{0.2 \times Y(p_i)}$$

where s_i is the sensitivity of the model to parameter i, $Y(\,)$ is the net nutrient flux for the given parameter set, and p_i is the parameter being adjusted (Ellner and Guckenheimer 2006). We analyzed the sensitivity of the full model to the estimated biomass density of YOY fish ($n_{YOY} \times mass_{YOY}$) with the same method, adjusting the asymptote and slope parameters by ±10% and recording the change to the full model.

Watershed loading model

To understand the impact that alewives are having on

their natal systems, we estimated background phosphorus loading into Bride Lake. Export coefficient models are widely used to estimate the nutrient loads from watersheds (Johnes 1996). These models use an estimate of the nutrient yield for each land-use type in a watershed to calculate the total nutrient load from the landscape (Reckhow and Simpson 1980). We used the Lake Loading Response Model, an export coefficient model that was developed for use in southern New England (AECOM Technology Corporation 2009). The Lake Loading Response Model considers water that flows overland (runoff) and subsurface (baseflow) and produces an estimate for the nutrient yield of a watershed based on precipitation, land uses, and basin characteristics. The model has been used by the CTDEP for Total Maximum Daily Load analysis of Linsley Pond, and it showed a close match to other estimates of nutrient loading (Stahl and Bolton 2005). The extent of the watershed of Bride Lake was determined using the National Hydrography Dataset and overlaid on land cover information from the 2001 National Land Cover Database to determine areal land uses (Homer et al. 2004). Although we do not have land-use information from the 1960s, the Bride Lake watershed likely has changed little due to the presence of two large prisons in the watershed.

Annual precipitation was calculated from monthly precipitation records from Middletown, Connecticut (42 km to the northwest of Bride Lake), from 1982 to 1996. Median values of loading estimates for each land use were chosen and nutrient inputs from the approximately 50 blue heron (*Ardea herodias*) individuals nesting in the watershed were included in the model. The proportion of phosphorus that makes it through the watershed to the lake, known as the phosphorus basin attenuation, was considered to be moderate due to the presence of a wetland in the basin (K. Wagner, AECOM Global Environment, P.O. Box 506, 11 Phelps Way, Willington, CT 06279, USA, personal communication (2009)). To ensure that the estimate of phosphorus loading was reasonable, the model output was entered into the equation

$$TP_{lake} = \frac{TP_{in}}{1 + 1.12(year^{-0.47}) \times \tau_w^{0.47}}$$

which estimates the lake phosphorus concentration (TP_{lake} (micrograms per litre)) using the inflow phosphorus (TP_{in} (micrograms per litre)) and the water residence time (τ_w (years)). Brett and Benjamin (2008) found this relationship to perform better than several older models relating phosphorus loading to lake phosphorus concentration. Predicted TP_{lake} was compared with measured values of TP_{lake} taken in the pelagic zone of Bride Lake during the summer months.

Results

Alewife nutrient loading model

Adult alewives contribute considerable amounts of phosphorus to Bride Lake. The values for all parameters used in the nutrient loading model are provided (Table 1). Each adult entering Bride Lake currently adds a mean of 0.46 g of phosphorus to the system. Adults that die in the system (P_{mort}) make up 83% of the total alewife phosphorus input, with each carcass contributing 0.68 g of phosphorus. Adults that survive each add 0.18 g of phosphorus, of which 67% is excretion ($P_{excretion}$) with gametes ($P_{gametes}$) contributing the remainder. The $P_{gametes}$ is split nearly evenly between males and females, as the higher phosphorus content of testes compensates for their lower mass. In the 1960s, adult alewives entering Brides Lake were larger than present-day alewives and contributed 39% more phosphorus per fish (mean of 0.64 g P·fish^{-1}). The difference in nutrient loading between the present and the 1960s is magnified when the size of the populations is taken into account. The average population returning to Bride Lake from 2003 to 2008 was nearly 90 000 fish, while in 1966 and 1967, the population averaged over 160 000 fish. As a result, the total amount of phosphorus added to Bride Lake in the 1960s was 2.5 times greater than it is today (Fig. 1).

YOY growth and survival

Growth and survival of YOY alewives in the Linsley Pond mesocosms was strongly density dependent (Fig. 2). Growth rate declined with increasing initial stocking densities as a negative exponential in the form of $Y = 0.0112 + 0.26 \times e^{-0.84x}$, where Y is growth rate (grams per day) and x is the initial density of YOY alewives stocked on 12 July 2005 ($n = 12$, $F_{2,10} = 36.57$, $r^2 = 0.89$, $p < 0.001$) (Fig. 2*a*). Survival declined with increasing initial stocking density. When one outlier was removed, a linear relationship between initial stocking density and daily mortality rate was found with $Y = 0.0006x - 0.0004$, where Y is the daily individual mortality rate and x is the initial density of YOY alewives ($n = 11$, $r^2 = 0.77$, $p < 0.001$) (Fig. 2*b*). The outlier was a treatment with two fish in which one died between days 14 and 35 of the experiment.

An asymptotic exponential function provided a good fit to the density-dependent growth of the YOY alewives, resulting in the relationship $n_{YOY} \times mass_{YOY} = 5.42\ g{\cdot}m^{-2} \times (1 - e^{-2.73x})$, where x is the initial stocking density of YOY alewife in the mesocosms ($n = 12$, $r^2 = 0.46$, $p < 0.01$) (Fig. 2*c*). After adjusting the asymptote for Bride Lake, the slope (decay constant) of the exponential decline of the YOY population in Bride Lake was found to be –0.13 day^{-1} to give an estimate of 6.39 YOY alewives surviving to 12 July (start of the mesocosm experiment) per adult spawner. After multiplying the density of fish by the area of the lake (28.7 ha), the resulting relationship between spawner density and the mass of YOY alewives in Bride Lake was $n_{YOY} \times mass_{YOY} = 2.67\ kg \times (1 - e^{-0.00061 \times n_s})$ (Fig. 1).

At the current escapement of 90 000 adults, the phosphorus export from YOY alewives is 2.66 kg and the net phosphorus input to Bride Lake by alewives is 38.6 kg. With the adult population of 162 000 found in 1960s, YOY export is expected to have been similar at 2.67 kg of phosphorus, but the net input would have been much higher with 100.8 kg of phosphorus imported to Bride Lake.

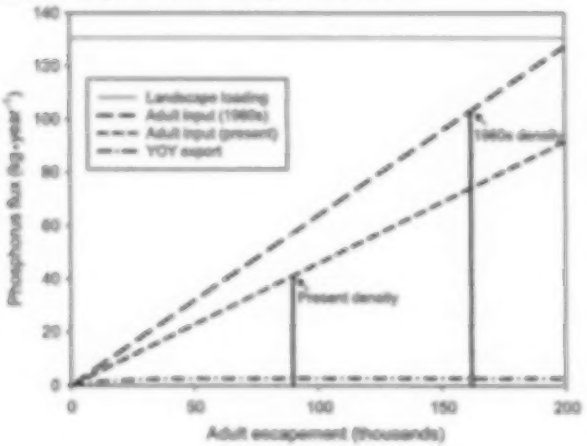
For Linsley Pond, we estimate a relationship between adult spawners and YOY biomass export of $n_{YOY} \times mass_{YOY} = 2.96\ kg \times (1 - e^{-0.00061 \times n_s})$, if early survival is the same as in Bride Lake. If the survival rate of fish less than 30 mm increased by an order of magnitude so each spawner resulted in 63.9 YOY alewives surviving to 12 July, the resulting relationship would be $n_{YOY} \times mass_{YOY} = 2.96\ kg \times (1 - e^{-0.00061 \times n_s})$ (Fig. 3). This estimate is reason-

Table 1. Parameters and sources for the alewife (*Alosa pseudoharengus*) nutrient loading model.

Trait	Value	Reference(s)
Adult numbers (n_a)	Variable	1, 2
Adult mortality rates (μ_a)	0.56·year^{-1}	2, 3
Adult wet mass ($mass_a$)	161.5 g (present), 222.4 g (1960s)	1, 2
Adult length ($length_a$)	260 mm (present), 289 mm (1960s)	1, 2
Adult P concentration ($[P_a]$)	0.0042 g P·g fish^{-1}	4
Adult fecundity (F_a)	3596 × $length_a$ – 766 187	1, 2
Egg wet mass ($mass_e$)	0.00012 g	1, 2
Egg P concentration ($[P_e]$)	0.0031 g P·g egg^{-1}	1
Δ testes wet mass ($\Delta mass_t$)	7.08 g (present), 11.60 g (1960s)	3, 5
Testes P concentration ($[P_t]$)	0.0088 g P·g testes^{-1}	3
Adult excretion rate (E_a)	2.17 μg P·g^{-1}·h^{-1}	6
Adult time in system (t_a)	14 days	2
YOY P concentration ($[P_{YOY}]$)	0.0058 g P·g YOY^{-1}	1

Note: 1, This study; 2, Kissil (1974); 3, Dalton et al. (2009); 4, Durbin et al. (1979); 5, J.P. Davis (CTDEP Inland Fisheries Division, Eastern District Headquarters, 209 Hebron Road, Marlborough, CT 06447, USA, unpublished data); 6, Post and Walters (2009).

Fig. 1. Phosphorus flux to Bride Lake from alewives (*Alosa pseudoharengus*) and landscape sources across a range of adult densities. Average current (2003–2008) and 1960s (1966–1967) adult alewife escapement indicated by vertical bars.



able, as Havey (1973) found an average of 366 YOY alewife emigrants per adult spawner when adult densities were low following the restoration of an alewife population in Love Lake, Maine.

Sensitivity analysis

For the Bride Lake nutrient loading model, adult population size and adult body size (n_a and $mass_a$), which affect the input from P_{mort}, $P_{gametes}$, and $P_{excretion}$, were the most sensitive parameters, with sensitivities of 1.07 and 1.12, respectively. Adult phosphorus concentration had a sensitivity of 0.88, while adult mortality was slightly less important with a sensitivity of 0.65. The parameters for $P_{gametes}$ (F_a, $mass_e$, $[P_e]$, $\Delta mass_t$, and $[P_t]$) had little impact on the net nutrient flux, with sensitivity values of just 0.03 each. The adult time in the lake and excretion rate (t_a and E_a) each had a sensitivity of 0.12. The asymptote of juvenile biomass density (a) had a sensitivity of 0.07, while the slope parameter (b) had nearly no effect on the overall model at the adult densities seen in Bride Lake.

Landscape loading model

The parameters used for the lake loading response model export coefficient model are listed in Table 2. The amount of phosphorus added annually to Bride Lake from external sources (excluding alewives) was 130.7 kg (Fig. 1). Of this, 117.6 kg of phosphorus was from the watershed, 8.6 kg was directly deposited on the lake from the atmosphere, and 4.5 kg was from waterfowl. The 38.6 kg input from alewives brings our total estimated phosphorus load to Bride Lake to 169.3 kg·year^{-1}. Comparing the phosphorus concentration of Bride Lake with the Brett and Benjamin (2008) model shows that our loading estimate is reasonable but is likely an overestimate of the true phosphorus load to the lake. The Brett and Benjamin (2008) model predicted a lake phosphorus concentration of 23.6 μg·L^{-1}, 11% greater than the observed average summer phosphorus concentration.

Discussion

The full model for nutrient loading by an iteroparous fish shows that alewives are loading substantial quantities of phosphorus to Bride Lake. Alewives currently import 23% of the total phosphorus input to Bride Lake, and this number increases to 44% for estimates from the 1960s. These numbers are relatively high compared to the phosphorus loading reported for sockeye salmon (*Oncorhynchus nerka*), which supply 3%–28% of lake phosphorus budgets in normal years, with a peak of 58% of the phosphorus budget for Lake Iliamna in a peak year for sockeye returns (Stockner 1987; Gross et al. 1998). Not surprisingly, the majority (83%) of the input from alewives is from alewives that die in the system. The nutrient input from alewives was much greater in the 1960s than at present because of both greater run size and larger body size in the 1960s than at present. Although fish were only 38% heavier and 80% more numerous in the 1960s, the combination resulted in 2.5 times greater phosphorus input by alewives in the 1960s than in the early 2000s. We do not know the size of the alewife run

Fig. 2. Patterns of density-dependent (*a*) growth, (*b*) mortality, and (*c*) biomass production for alewives (*Alosa pseudoharengus*) in the Linsley Pond mesocosm experiment. The triangle in Fig. 2*b* was excluded from the analysis of density-dependent mortality.

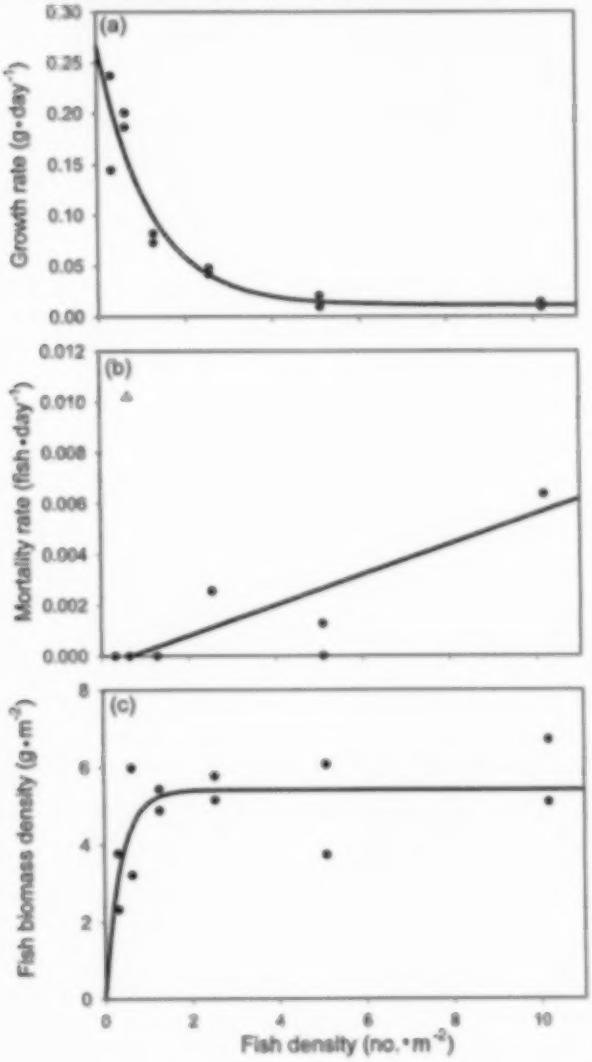
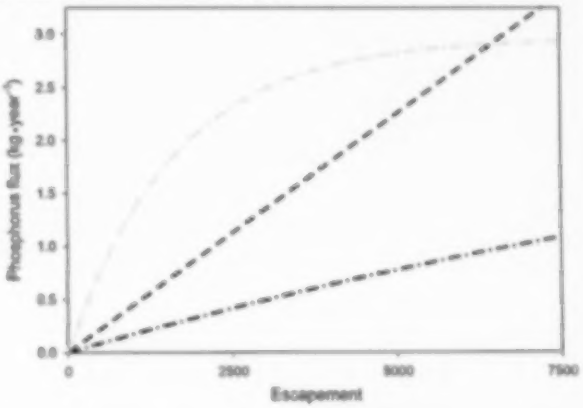


Fig. 3. Estimated phosphorus flux due to alewives (*Alosa pseudoharengus*) in Linsley Pond following restoration. YOY export predicted from juvenile growth in mesocosms with 6.39 YOY per spawner surviving to 12 July (black dot–dashed line) and 63.9 YOY per spawner surviving to 12 July (gray dot–dashed line). Input by adults is for current fish (black dashed line). Note that axes scales differ from those on Fig. 1.



before European settlement, but landscape nutrient inputs were likely considerably less (Brugam 1978) and alewife run size considerably larger, suggesting that alewives were an even more important part of the nutrient budget of coastal lakes in precolonial New England.

Based on the in-lake-survival of YOY alewives observed for Bride Lake, we believe that alewives are rarely nutrient exporters for a watershed. The growth of YOY alewives in mesocosms was strongly density dependent, but the early survival rates that we measured in Bride Lake were too low to produce a sufficient number of young to exceed the nutrient inputs of the parents. If, however, growth and survival of juveniles smaller than 30 mm are strongly density dependent, then it is possible that alewife populations could be a net exporter of phosphorus when adult populations are small. If 63.9 juveniles per adult survive to 12 July in Linsley Pond, rather than the 6.39 per adult estimated from early survival in Bride Lake, we estimate that the population will be a net exporter of phosphorus until the population reaches 6500 adults (690·ha^{-1}). Although they have not yet reached Linsley Pond, more than 3100 fish ascended the Branford fishway into the Branford Supply Ponds the first year that it opened (D.M. Post, unpublished data). If these fish had moved into Linsley Pond rather than remaining in the artificial supply ponds, we predict they would have imported 0.8 kg of phosphorus to Linsley Pond and, with good early survival, they could have exported greater than 1 kg of phosphorus. Thus, early in the recovery of an alewife population, net loading is likely to be small or even slightly negative (net export) where YOY survival and growth are high.

One possible source of bias in our estimates of nutrient export by YOY alewives is that juveniles can leave their natal lakes at different times throughout the year. The loss of some individuals early in the year may release the remaining fish from density dependence and increase the total biomass of YOY fish that emigrate from the system. For Bride Lake, Linsley Pond, and many other coastal lakes with low-gradient outlet streams, the outlet streams often go dry for most of the summer months, prohibiting emigration. In wet years and in lakes with larger outlet streams, YOY alewives can migrate to the ocean throughout the summer. Yako et al. (2002) found that alewives in lakes where they cannot emigrate throughout the year were smaller, possibly due to an increase in intraspecific competition throughout the growing season. As a result, managing flow regimes to allow alewife emigration throughout the summer may both benefit alewife populations and increase nutrient export from eutrophic systems.

In the Bride Lake model, sensitivity analysis shows that at current levels of adult escapement, parameters related to phosphorus input by adult mortality are the most important to nutrient loading. Adult escapement and adult body size

Table 2. Parameters for the Bride Lake export coefficient model.

Land use	Area (ha)	Runoff fraction	Baseflow fraction	Runoff P export ($kg \cdot ha^{-1} \cdot year^{-1}$)	Baseflow P export ($kg \cdot ha^{-1} \cdot year^{-1}$)	Notes
Low-density residential	40.23	0.40	0.25	1.10	0.010	>0.4 ha lot
Medium-density residential or highway corridors	8.28	0.50	0.15	2.50	0.010	0.1–0.4 ha lot
High-density residential or commercial	1.26	0.60	0.05	2.50	0.010	<0.1 ha lot
Institutional, cemetery, park, or recreational	66.87	0.40	0.25	1.10	0.010	
Agricultural, row crops	1.26	0.3	0.3	1.00	0.010	
Agricultural	36.45	0.3	0.3	0.40	0.010	
Upland	377.91	0.3	0.4	0.05	0.004	
Wetland/lake	55.10	0.05	0.4	0.20	0.004	
Meadow	25.65	0.15	0.3	0.20	0.004	

Note: Other model parameters: precipitation 1.3 $m \cdot year^{-1}$ (Middletown, Connecticut), waterfowl 4.5 kg $P \cdot year^{-1}$ (50 birds), water basin attenuation 0.8, and P basin attenuation 0.6.

have the highest sensitivities, as they are important for all input terms. Adult mortality also has a very strong impact, although considerably less than population size or body size because although an increase in adult mortality increases the phosphorus input from mortality, it decreases the input from gametes and excretion. Since adult population size, adult body size, and adult mortality are expected to vary considerably from system to system, it is important that they are accurately measured to get a good estimate of net phosphorus loading from alewives. Since the model is not very sensitive to any of the factors affecting the phosphorus load from gametes or excretion and these factors are not expected to vary greatly between lakes, these parameters are less important to measure in different systems. One exception is the time of adult residence in freshwater, which may vary considerably between lakes and could have a strong effect on the amount of excretion and the overall model if differences are on the order of weeks. Since the YOY production is a small fraction of the net nutrient flux at the current escapement levels for Bride Lake, the YOY biomass density asymptote has little effect on the overall nutrient budget. In the Bride Lake model, the slope parameter has virtually no effect, since the population is near the asymptote of YOY biomass density. In lakes that have smaller adult populations, however, this parameter is very important to the overall nutrient budget. In the projected nutrient budget for Linsley Pond, for example, the model is very sensitive to the slope parameter of the YOY export term.

Knowing the nature of the nutrient flux from alewives to coastal ponds will allow for adaptive management of alewife populations for one of two goals: minimizing nutrient inputs while allowing some alewives to spawn or maximizing alewife returns while limiting nutrient loading. In Linsley Pond, for example, managers can control the number of alewives that ascend the Branford Supply Ponds fishway. Once a run of alewives becomes established in the pond, managers could constrain the number of fish that are allowed into the pond to a point where there is nearly zero net loading or at a point where YOY export is nearly maximized. Since juvenile growth is strongly density dependent, changing the number of adults will not have a large effect on the biomass of juveniles that survive to emigrate from the pond, although the number of juveniles will be affected. If early survival of alewives in Linsley Pond is similar to that in Bride Lake, capping the adult run at 23 000 fish ($2450 \cdot ha^{-1}$), the YOY biomass exported would be expected to be greater than 75% of the maximum capacity for the lake. The net nutrient input for this many fish would be 8.3 kg of phosphorus, which is less than 10% of the current phosphorus load to the pond.

The nutrient loading estimate from adult mortality that we provide is an upper estimate for the nutrient load to lakes, as some of the nutrients from carcasses can be removed from the system by mobile predators. At present, cormorants (*Phalacrocorax auritus*) are a major predator of adult alewives, responsible for as much as 48% of the alewife mortality in Bride Lake (Dalton et al. 2009). Although the birds transport much of the nutrients away from the lake as allocation to growth and reproduction or as feces, they excrete a substantial proportion of their diet back into the lake, since they remain on the lake for the majority of the day. The nutrients excreted by cormorants are not available for direct uptake by primary producers, as excretion from fish is, but feces are mineralized by microbes to available forms (Vanni 2002). Aside from mobile predators, the retention of carcasses in the lake should be high, unlike in lotic systems where water flow necessitates an explicit consideration of carcass retention (Garman 1992; Nislow et al. 2004).

We estimate that 11% of the phosphorus input from alewives is due to excretion of alewives that survive spawning. Since adult mortality is likely not instantaneous, an additional 5.9 kg of phosphorus could be excreted in the lake by fish that eventually die, bringing the total contribution from excretion to as much as 26% of the total alewife phosphorus input. This estimate closely approximates that of Durbin et al. (1979) who found that 18% of alewife phosphorus input came from excretion. The importance of inputs from metabolic processes from anadromous fish has received relatively little attention, likely because it is not important to the net energy budget of semelparous species. Recent work in Bride Brook, which drains Bride Lake, has shown that alewife excretion is an important source of nutrients for the stream (Walters et al. 2009). Although Bride Lake is many times larger than the stream, the residence time for alewives in the lake is considerably longer than in the stream, resulting

in more nutrients being excreted. Excretion from surviving alewives alone equals 3% of the external load of the phosphorus to the lake at present and would have been 5% in the 1960s. The claim of Johnston et al. (2004) that *Oncorhynchus* spp. do not excrete phosphorus when they are not feeding is not relevant to breeding individuals, whose physiology changes dramatically as they prepare to spawn (Gende et al. 2002). A recent meta-analysis shows a striking difference in nitrogen and phosphorus dynamics between natural salmon runs and artificial carcass additions (Janetski et al. 2009). The additional nutrients seen in the natural system may be coming from excretion before senescence. Since excretion is in an inorganic form that can be readily used by primary producers, it appears that excretion may be an important but often overlooked piece of the nutrient budget for anadromous fish (Post and Walters 2009).

The decline in the size of existing alewife runs has led to the listing of alewife as a species of special concern (National Marine Fisheries Service 2006). By providing passage past existing barriers, fisheries managers have the opportunity to restore fish populations and strengthen the overall anadromous alewife population. For most diadromous fish whose populations are declining, restoration would be a desirable outcome and environmental groups would rally for the demolition of dams or the installation of fish ladders. Alewives, however, face the additional obstacle of being embedded in the densely populated coast of eastern North America where the nutrients that they import are an unwelcome addition to lakes that are already eutrophic. Although this makes alewife restoration projects more challenging, alewife populations can be adaptively managed to minimize the extent of potentially harmful nutrient loading.

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Reproductive interactions between fugitive farmed and wild Atlantic cod (*Gadus morhua*) in the field

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Abstract: Atlantic cod (*Gadus morhua*) are being increasingly farmed in net pens adjacent to coastal populations that are currently at historic lows. One concern is that farmed escapees enter local spawning shoals and mate with wild cod. We tested for the potential of escaped farmed cod to interact and hybridize with wild fish by examining the spatial dynamics of, and associations between, fish tagged with ultrasonic transmitters. Based on these data, we also investigated the basic mating system of cod in the field. The spawning ground was best described as a lekking arena. Wild males aggregated near the seafloor and associations between individuals were frequent. Wild females had a pelagic and dispersed distribution and rarely associated with each other. Associations between individual wild males and females were also infrequent. Farmed males rarely associated with wild fish and had core usage areas above the wild males, suggesting that they were not admitted into the spawning arena. Farmed females were over the spawning arena more frequently than wild females and often associated with wild males at the depth of the spawning arena, indicating potential mating with wild males and the possibility of courtship interference. Hence, hybridization between escaped farmed and wild cod is likely.

Résumé : On fait de plus en plus d'élevages de morues (*Gadus morhua*) dans des enclos en filet près des populations côtières qui se retrouvent actuellement à des densités historiquement basses. On se préoccupe de ce que des poissons échappés d'élevage se joignent aux bancs locaux de reproducteurs et frayent avec des morues sauvages. Nous avons testé la possibilité que des morues échappées d'élevage interagissent et s'hybrident avec les poissons sauvages en examinant la dynamique spatiale et les associations de poissons marqués d'une étiquette émettrice d'ultrasons. Avec ces données, nous avons aussi étudié le système d'appareillade de base des morues en nature. Les zones de fraie peuvent le mieux être décrites comme des arènes de lek. Les mâles sauvages se rassemblent près du fond marin avec de fréquentes associations entre individus. Les femelles sauvages ont une répartition pélagique et dispersée et s'associent rarement l'une à l'autre. Les associations entre des individus sauvages mâles et femelles sont aussi peu fréquentes. Les mâles d'élevage s'associent rarement aux poissons sauvages et leurs zones principales d'utilisation se situent au-dessus de celles des mâles sauvages, ce qui laisse croire qu'ils ne sont pas admis dans l'arène de fraie. Les femelles d'élevage se retrouvent au-dessus de l'arène de fraie plus fréquemment que les femelles sauvages et s'associent fréquemment à des mâles sauvages dans le fond de l'arène de fraie, ce qui indique la possibilité d'une appareillade avec les mâles sauvages et de comportements de cour d'interférence. L'hybridation entre les morues échappées de culture et les morues sauvages est donc probable.

[Traduit par la Rédaction]

Introduction

The number of accidental and intentional releases of hatchery-produced fish into marine environments is increasing, driven by declines in exploited wild stocks and subsequent development of mariculture, stock enhancement, and restocking (Brown and Laland 2001; Naylor et al. 2005). However, there is surprisingly little known of the natural reproductive behaviour of many of these species, particularly of oceanic spawners. Many of the current candidate species for mariculture such as flatfishes, sparids, sciaenids, scombrids, and gadoids (Food and Agriculture Organisation of the United Nations (FAO) 2007) spawn at night or at depths that prevent direct observation. They also attain sizes at maturity that can make observations in the laboratory difficult. Without this knowledge, it is difficult or impossible to predict the reproductive success of farmed fish in the ocean. Resolving the behaviour of individual fish that move rapidly

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in three dimensions under low-light conditions in the ocean is difficult in itself, but elucidating social and reproductive interactions between these fish has presented itself to be a formidable challenge.

Much more is known of the natural reproductive behaviour of anadromous or freshwater fish such as salmonids. Domestication has caused rapid phenotypic and genotypic divergence between farmed and wild salmonids (Gross 1998; Huntingford 2004), and escaped farmed salmonids interbreed with wild stocks, causing genetic introgression and fitness depression in wild populations (McGinnity et al. 2003; Araki et al. 2007). In Atlantic salmon (*Salmo salar*), this gene flow is biased towards farmed females that are readily accepted by wild males (Fleming et al. 1996, 2000), whereas farmed males are outcompeted by wild males (Fleming et al. 1996; Weir et al. 2004). Interference of wild courtship or spawning behaviour by farmed salmon also differs between the sexes, depending on factors such as the intensity of competition for breeding resources, nesting behaviour, and the timing of spawning (Lura and Sægrov 1991; Fleming et al. 1996, 2000). Hence, the risks imposed from escapees of other farmed species to wild populations are also likely to be sex-biased, particularly for species for which the intensity of mating competition and mate choice is sexually asymmetric.

Atlantic cod (*Gadus morhua*) are such a species (Brawn 1961; Hutchings et al. 1999; Rowe et al. 2008) and are being farmed at an increasing rate throughout the North Atlantic (Rosenlund and Halldorsson 2007). In captivity, the cod mating system involves agonistic interactions between males and courting of females with behavioural displays and acoustic vocalisations (Brawn 1961; Hutchings et al. 1999; Rowe et al. 2008). Coastal cod (i.e., nonmigratory coastal populations) have strong fidelity to known spawning locations, where the shoals may persist for months (Robichaud and Rose 2001, 2003; Espeland et al. 2007). The high residency of these populations in sheltered areas makes it possible to track individually tagged fish with hydrophone arrays, and experimentally released farmed cod are known to navigate to local spawning grounds (Svåsand et al. 1990; Wroblewski et al. 1996; Uglem et al. 2008). Coastal cod are hence an ideal system for detailed investigation of behavioural interactions between farmed and wild fish in the ocean. There is also major concern about the impact of farm escapees on coastal cod populations (Moe et al. 2007) that have a localized genetic structure (reviewed by Bekkevold et al. 2006) and are already at historically low levels (Hutchings and Baum 2005; Berg 2007).

We investigated the fine-scale spatial dynamics of farmed and wild cod on a natural spawning ground by individually tagging fish with ultrasonic transmitters and tracking them with a stationary positioning system. We quantify, for the first time, associations between farmed and wild fish on a natural spawning ground. Using this data, we (*i*) examine the basic mating system of coastal wild cod and (*ii*) evaluate the likelihood that farmed fish hybridize with their wild counterparts. A previous study comparing the vertical dynamics and reproductive behaviour of farmed and wild Norwegian coastal cod showed that wild males maintained positions closer to the seafloor and considerably deeper than females and farmed males (Meager et al. 2009). Hence, in the present study, we test the prediction that farmed females but not farmed males enter wild spawning shoals.

Materials and methods

Study site and experimental fish

The study was conducted on a known spawning ground of coastal cod at Austevoll, western Norway (Fig. 1), from 19 February to 25 March 2007. In the centre of a spawning ground of approximately 20 ha in area, the main spawning aggregation (termed "spawning arena") covers an area of approximately 2 ha and is associated with a rocky slope from depths of 30 to 68 m.

During the study period, day length ranged from 9 h 29 min to 12 h 38 min, and maximum diurnal irradiance at the water surface ranged from 42 to 1437 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Water currents were slow (0–6.8 $cm \cdot s^{-1}$) and tidally driven. Temperature was stable at around 8 °C in water deeper than 20 m, but cooler in surface waters (<20 m depth, 5.9 ± 0.71 °C, mean ± standard deviation, SD) (J.J. Meager, unpublished data).

Wild coastal cod were caught on the spawning ground using fish traps and nets at depths of 5 to 25 m from mid-December 2006 to early February 2007. Captured fish were brought slowly to the surface to prevent barotrauma and were kept in two sea pens (1 m diameter, 4 m depth) at a location 2.8 km from the study site.

Farmed fish were obtained at harvest size from a commercial cod farm at Fitjar (59°58′N, 5°21′E, ~12.5 km away) and transferred to two sea pens (1 m diameter, 4 m depth) adjacent to the wild cod in January 2007. These fish were age 3 and had previously spawned at age 2 (Skjæraasen et al. 2008). They were transferred from the hatchery to sea pens (15 × 15 m, 12 m deep net pen) as juveniles at densities from 3 to 6 $fish \cdot m^{-3}$ and surface fed with commercial pellets. The parental fish were wild-caught nearby at Bømlo (59°53′N, 5°5′E) during 2001 and were in captivity for three years.

In mid-February 2007, fish were anaesthetized with 0.5 $g \cdot L^{-1}$ Benzocaine. Ultrasound was then used to assess reproductive status and sex (following Karlsen and Holm 1994), using a scanner with a 7.5 MHz transducer (Dynamic Imaging Ltd., Livingston, Scotland, UK). Fish were then individually tagged with external Floy T-bar tags inserted into the musculature adjacent to the first and second dorsal fins, and total length and body weight were recorded. Ultrasonic tags (full description below) were intraperitoneally implanted into 48 fish (12 of each sex and origin) that matched the following criteria: (*i*) one week or less from spawning based on the ultrasound image and (*ii*) absence of morphological abnormalities or parasites that may affect behaviour.

Fish were size-matched as closely as possible (Table 1). Farmed female cod were of similar length and weight to wild female cod (length, separate-variance t test, $t = -1.27$, $df = 11.7$, $p = 0.22$; weight, Student's t test, $t = -0.64$, $df = 22$, $p = 0.54$). Wild males were on average 4 cm longer (i.e., 6% longer) than farmed males (separate-variance t test, $t = -2.35$, $df = 13.2$, $p = 0.035$), but of similar weight (separate-variance t test: $t = -0.39$, $df = 14.6$, $p = 0.7$).

Fish were allowed to recover in aerated tanks for approximately 1 h after surgery and were continuously monitored

Fig. 1. Location of study area in (*a*) Norway and (*b*) western Norway. (*c*) The locations of the hydrophone receivers at the study site are indicated by the buoy symbols. Depth isobaths (10 m) were determined by echosounding surveys and interpolated by kriging.

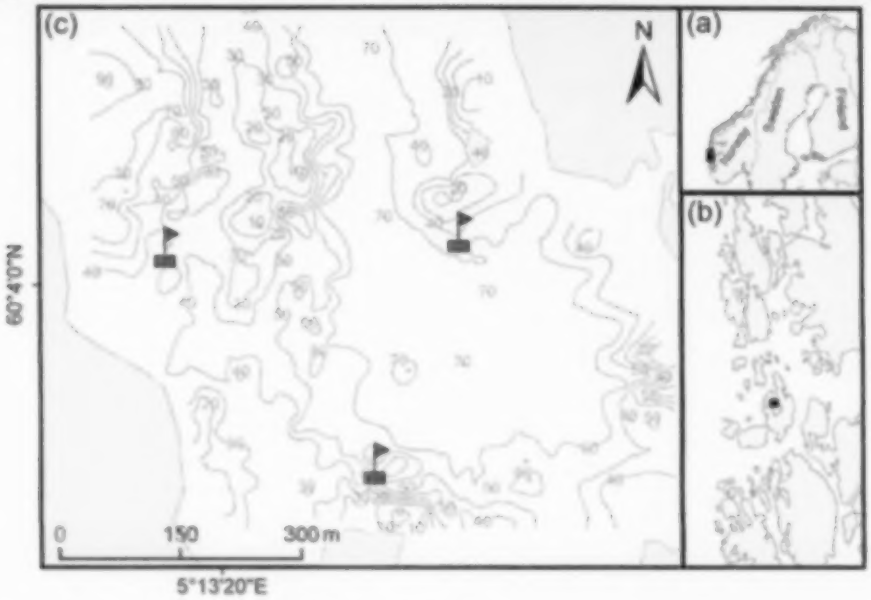


Table 1. Details of fish tagged with ultrasonic transmitters.

Tag type	Origin and sex	*n*	Standard length (mean ± SD, cm)	Weight (mean ± SD, kg)	Condition (mean ± SD)
Coded	Farmed ♀	10	61.8±1.6	3.42±0.49	1.45±0.20
Coded	Farmed ♂	10	61.2±1.9	2.90±0.39	1.26±0.07
Coded	Wild ♀	10	65.2±9.6	3.18±1.80	1.07±0.04
Coded	Wild ♂	10	66.0±6.6	3.09±1.02	1.05±0.06
Continuous	Farmed ♀	2	62.5±2.1	3.53±0.57	1.44±0.09
Continuous	Farmed ♂	2	63.5±0.8	3.26±0.18	1.27±0.08
Continuous	Wild ♀	2	65.0±1.4	2.85±0.06	1.04±0.06
Continuous	Wild ♂	2	65.5±3.5	3.02±0.48	1.07±0.002

Note: Fish were tagged with either continuous tags (Continuous) that transmitted data every second on separate frequencies or coded tags (Coded) that transmitted individually coded data at random intervals between 150 and 250 s on a single frequency. Condition was calculated as Fulton's K (weight/length^3). SD, standard deviation.

for any signs of stress. They were then transferred back to the net pens for four to five days of further recovery before release at the spawning ground on 19 February. The main spawning period at this location is from mid-February to mid-March (information from local fishermen). Shortly after release, cod spawning was confirmed at the site by (*i*) the presence of recently fertilized eggs and (*ii*) hydrophone recordings of male mating calls (J.E. Skjæraasen, unpublished data).

Biotelemetry

We used a radio-linked stationary positioning system (VRAP, Vemco Ltd., Shad Bay, Nova Scotia, Canada) to track the ultrasonically tagged cod. The positioning system had a fixed array of three hydrophone receivers and used the arrival times of acoustic pulses to track fish in real time. The hydrophone buoys were anchored to the sea floor in a triangular configuration with 310–375 m between the buoys and encompassed an area of approximately 5.5 ha (Fig. 1).

Two separate transmitter systems were used: continuous tags (Vemco V16P-4H) that enabled tracking at a high-temporal resolution on a limited number of separate frequencies and individually coded tags (Vemco V16P-4H S256) that allowed a large number of fish to be tracked on the same frequency with longer intervals between positions (Meager et al. 2009). Eight continuous tags (two fish of each sex and origin) operated on separate frequencies from 51 to 81 kHz, and 40 coded tags (10 fish of each sex and origin) operated at 69 kHz. In this paper, we use alphanumerical codes to denote sex, origin (i.e., F, farmed; W, wild) and tag identity (four numbers, continuous transmitters; three numbers, coded transmitter). For example, W♂9658 is a wild male with continuous tag number 9658.

All tags were equipped with a hydrostatic-pressure sensor (depth sensor) and weighed 12 g in water (diameter, 16 mm;

length, 71 mm). Coded tags had a random delay of between 150 and 250 s between transmissions to minimize collisions between tag signals. In the worst-case scenario, with all tags within range of the system simultaneously, the average sampling interval was estimated to be 13.3 min (range, 3.8–44.2 min). In reality, the sampling interval was much shorter (i.e., 150–300 s) because all fish were not within range simultaneously. Continuous tags transmitted data every second but were tracked at an interval of 144 s because the system cycled between the eight separate tag frequencies, each time listening for 10 s and uploading data for 8 s.

Because the VRAP system tracks one frequency at a time, we cycled between tracking coded and continuous transmitters. After fish were released on 19 February, coded tags were tracked for the first 24 h, and continuous tags were tracked for the next 24 h. From 21 February to 25 March, we cycled between tracking coded tags for 72 h and continuous tags for 24 h.

The VRAP software (version 5.1.4, Vemco Ltd.) positioned fish based on the average of the 80% best-aligned acoustic pulses. To further filter positions for errors in positional calculation, we excluded positions where (*i*) distance from the nearest receiver buoy exceeded 1 km and (*ii*) $\sqrt{D}/p \geq 5$, where D was the standard deviation between pulses in a set of aligned data and p was the number of pulses received that could be assumed to originate from the same transmitter (Zamora and Moreno-Amich 2002). Filtered positions were then converted to geodetic coordinates using reference points recorded with a GPS (global positioning system; Garmin Ltd.) and transferred to a GIS (geographical information system) using ArcGIS (version 9.2, ESRI, Redlands, California). Positions from the first 6 h were removed from the data to exclude the initial postrelease responses of fish. Swimming speeds were estimated for fish that were repositioned within a 5-min time interval and were calculated as the straight-line distance divided by the time between two consecutive positional fixes.

Spatial analysis

We analysed the spatial movement patterns of individual fish and compared space use and overlap between fish of both sexes and origin (farmed or wild) using kernel modelling of utilization distributions (UD). This analysis focuses on the 28 individual fish that were positioned more than 30 times (10 wild ♂, 9 wild ♀, 5 farmed ♀, and 4 farmed ♂). The vertical dynamics of the fish tracked in this study have been analysed in detail elsewhere (Meager et al. 2009). Briefly, wild males were close to the seafloor and considerably deeper than females and farmed males, which had a pelagic distribution.

The 95% usage area (UD_{95}) was the area enclosed by the 95% UD isoline and was where a fish spent 95% of its time on the spawning ground (i.e., 95% chance of finding the fish within that area). Core usage areas (UD_{50}) were defined by the 50% isoline for each UD and corresponded to the core activity centres for each fish (Rodgers et al. 2007). A standard Gaussian fixed-kernel density estimator was used with standardized variances and "href" as the smoothing function (Worton 1987; Rodgers et al. 2007). To reduce autocorrelation and standardize data from continuous and coded transmitters, we subsampled the data for continuous transmitters at 10-min intervals before calculating the kernel UDs. We compared mean home range size (UD_{50} and UD_{95}) between origin and sex types with two-way, fixed-effect analyses of variance (ANOVAs), weighted by the number of observations used to calculate each UD (i.e., WLS GLM in SPSS 15.0, SPSS Inc., Chicago, Illinois). Variances were stabilized by log transformation. The same test was used to compare home-range fragmentation (following Hodder et al. 2007) between fish sex and origin, but the response variable here was the number of separate UD_{50} nuclei for each individual, normalized by a square-root transformation.

Spatial organisation within each group (sex–origin, *i*) was described with an overlap index (OI) that described the "uniqueness" of individual space use and varied from complete separation at 0 to complete overlap at 1, calculated as

$$(1) \quad OI_i = 1 - (\sum O_{ij} / \sum UD_{50ij})$$

where O_{ij} was the orthogonal UD_{50} usage area of individual j of sex–origin type i, i.e., the exclusive UD_{50} area that did not overlap with any other fish of type i. We then described static spatial overlap between individual fish with a utilization distribution overlap index (UDOI). This measured the percentage of UD overlap in all 378 possible pairs of 28 individual fish (termed "dyads"). For each dyad i of fish 1 (j) and fish 2 (k), UDOI was calculated for both UD_{50} and UD_{95} as

$$(2) \quad UDOI_i = 100 \times overlap_i / (area_j + area_k - overlap_i)$$

The same approach was used to calculate the percentage overlap of depth ranges (95% confidence intervals) of fish in each dyad. Overlap volume for each dyad was estimated by the product of UD_{95} overlap and depth range overlap and was also converted to an overlap percentage. Overlap indices were normalized by arcsine transformation and compared using linear mixed-effect models (LME), because individual fish were treated as random effects. We used a crossed-effects design in the "lme4" package (version 0.999375-27) of R 2.8.0 (R Foundation for Statistical Computing, www.r-project.org) to take into account the variance associated with individual fish in a given dyad (Faraway 2006):

$$(3) \quad y_{ij} = \mu_0 + \beta_{0j} + b_{F1i} + b_{F2i} + e_{ij}$$

where y_{ij} is the overlap index for dyad i of association type j (sex–origin), μ_0 is the general intercept, β_{0j} is the fixed effect of association type, b_{F1i} is the random effect of fish 1, b_{F2i} is the random effect of fish 2, and e_{ij} is unexplained error. The association type effect included the 10 different dyadic combinations of fish sex and origin. A priori contrasts were used to compare farmed–farmed and farmed–wild overlap against the control (wild–wild dyads) for the three groups of sex associations (male, male–female, and female). In all LME analyses, stepwise term deletion and log-likelihood ratio tests (G^2) were used to arrive at the final models (Faraway 2006).

Spatial dynamics of females

As previous studies have indicated that female cod enter male spawning shoals to spawn (Brawn 1961; Hutchings et al. 1999; Nordeide and Folstad 2000), we tested for differ-

ences in the frequency of visits to the spawning arena by farmed and wild females. The spawning arena was defined as the total area covered by the wild male UD_{50} core usage areas and closely corresponded to the location identified by local fishers as the main spawning aggregation in the area. The frequency of visits by farmed and wild females was compared using a generalized linear mixed-effect model (GLMM of the lme4 package of R) with a longitudinal random effect:

$$(4) \quad \text{logit}(p_{ijt}) = \mu_0 + \beta_{0j} + b_{ti} + \epsilon_{ijt}$$

where p_{ijt} is the probability of positioning fish i of origin j (farmed or wild) over the spawning arena on day t, μ_0 is the general intercept, β_{0j} is the fixed effect of origin, b_{ti} is the random effect of an individual fish, and ϵ_{ijt} is unexplained error. The response variable was coded as either on (1) or off (0) the spawning arena and was modelled with a binomial error (logistic link function). All females with sufficient positions (11 farmed ♀ and 11 wild ♀) were included in this analysis.

Analysis of spatial–temporal associations

We analysed the full data set of all 45 fish that were positioned (12 wild ♂, 11 wild ♀, 11 farmed ♂, and 11 farmed ♀ fish) for associations between fish at a scale likely to represent social interactions rather than random encounters. This was done with a program written in Matlab 7 (MathWorks Inc., Natick, Massachusetts) that searched through a matrix of all possible dyadic combinations of fish positions that overlapped in time and space. Time and three-dimensional Euclidean distance between positions were used as the criteria for an association because of limitations in the temporal and spatial resolution of the system (approx. ±1 m^2; O'Dor et al. 1998; Espeland et al. 2007). Time–distance thresholds were chosen to optimize the balance between missing real behavioural interactions (with small thresholds) or detecting false associations (with larger thresholds). Initial examination of the relationship between these thresholds and the number of associations detected indicated that this choice was more critical for distance, because the number of associations detected increased linearly with distance but quickly reached an asymptote with time. The time–distance thresholds selected were 5 min and 10 m (AS_{10}). Ten metres corresponds to an estimated horizontal sighting distance towards the side profile of a 70 cm fish at a depth of 35 m during an average day during the spawning season in western Norway (J.J. Meager, unpublished data). For comparison, we also present the results of associations at 5 min and 5 m (AS_5).

As positioning frequency differed between individuals, we standardized AS_{10} as the proportion of sampling density for each dyad. Sampling density was calculated as the number of times that a given dyad was positioned within each 5-min period. We tested for differences in standardized AS_{10} between association types using a mixed-effect model following eq. 3. The response variable in this analysis was binomial, representing a pair of fish positioned within a 5-min interval that were either associated ($AS_{10} = 1$) or not associated ($AS_{10} = 0$) and was therefore modelled with a GLMM. In theory, fish that swim faster encounter other fish more often. Therefore, we also ran this analysis using dyad swimming speed as a covariate, which was calculated as the product of mean swimming speeds of each fish (body lengths·s^{-1}).

We tested if the depth of association (AS_{10}) deviated from fish depth at other times by adding a term that described association type to the LME used by Meager et al. (2009) in their analysis of vertical dynamics. Briefly, the fixed effects in this LME were association category (association or no association), sex, origin (farmed or wild), and diel period (day or night), and the random effect was nested to control for diel and daily variation in the depths of individual fish.

Results

Spatial patterns: utilization distribution

Twenty-eight fish had sufficient position fixes for spatial analysis ($n > 30$, 10 wild ♂, 9 wild ♀, 5 farmed ♀, and 4 farmed ♂). The range in size of utilization distributions was from 1.7 to 50.8 ha for UD_{95} and from 0.2 to 11.4 ha for UD_{50}. Utilization distribution size was affected by the sex (UD_{95}, $F_{[1,24]} = 15.8$, $p = 0.001$; UD_{50}, $F_{[1,24]} = 6.2$, $p = 0.02$) and origin (UD_{95}, $F_{[1,24]} = 5.2$, $p = 0.031$; UD_{50}, $F_{[1,24]} = 11.0$, $p = 0.03$) of fish, but not by a sex × origin interaction (p values from 0.24 to 0.42). On average, utilization distributions (UD_{95}) were 30% larger and core usage areas were 34% larger for females than for males. Wild fish had, on average, 12% larger utilization distributions and 8% larger core usage areas than farmed fish. The core home ranges of wild fish tended to be more fragmented than those of farmed fish ($F_{[1,24]} = 4.21$, $p < 0.051$), but there was neither a difference between sexes nor an interaction between fish origin and sex (p values from 0.44 to 0.72). One wild male (W♂9658) had three home range nuclei, nine fish had two nuclei (3 wild ♂, 4 wild ♀, and 2 farmed ♀), and the other 18 fish had one nucleus.

Core usage UD_{50} areas of wild males were highly overlapping across an area of 15.3 ha with a within-group overlap index (OI) of 0.48. Overlap was greatest at the centre of the study site (Fig. 2) at a site corresponding to a rocky slope from 34 m to 70 m deep. An additional area of UD_{50} overlap of three wild males occurred 150 m away (Fig. 2) on a slope from 30 m to 65 m deep. The core usage areas of wild females covered a larger area of 26.1 ha, and within-group overlap was less than that of wild males (OI = 0.34; Fig. 2). Farmed fish tended to have the lowest within-group overlap (farmed males, UD_{50} covered 13 ha, OI = 0.13; farmed females, UD_{50} covered 15.2 ha, OI = 0.25; Fig. 2).

Mean dyad UD overlap (UDOI) did not significantly differ between sex–origin types (UD_{95}, $G^2 = 9.65$, df = 9, $p = 0.4$; UD_{50}, $G^2 = 4.86$, df = 9, $p = 0.85$; Fig. 3*a*). On average, UD_{95} dyad overlap was high regardless of sex–origin type (18%–31%) and low for core UD_{50} usage areas (1% to 8%) (Fig. 3*a*). The percentage of depth overlap was, however, significantly affected by the dyad type (sex–origin type, $G^2 = 20.3$, $p = 0.016$). Farmed females dyads had the greatest overlap ($t = 3.3$, $p < 0.0001$, compared with wild ♀–♀ control), and there was no depth overlap between wild and farmed males (Fig. 3*b*). Patterns of significance were very similar for the volume overlap index (effect of sex–origin type, $G^2 = 27.2$, $p < 0.001$).

Fig. 2. Core home ranges (UD_{50}, 50% utilization distributions) of fish of each sex and origin (10 wild ♂, 9 wild ♀, 5 farmed ♀, and 4 farmed ♂). The hydrophone receivers are indicated by the buoy symbols and the scale of each panel is identical.

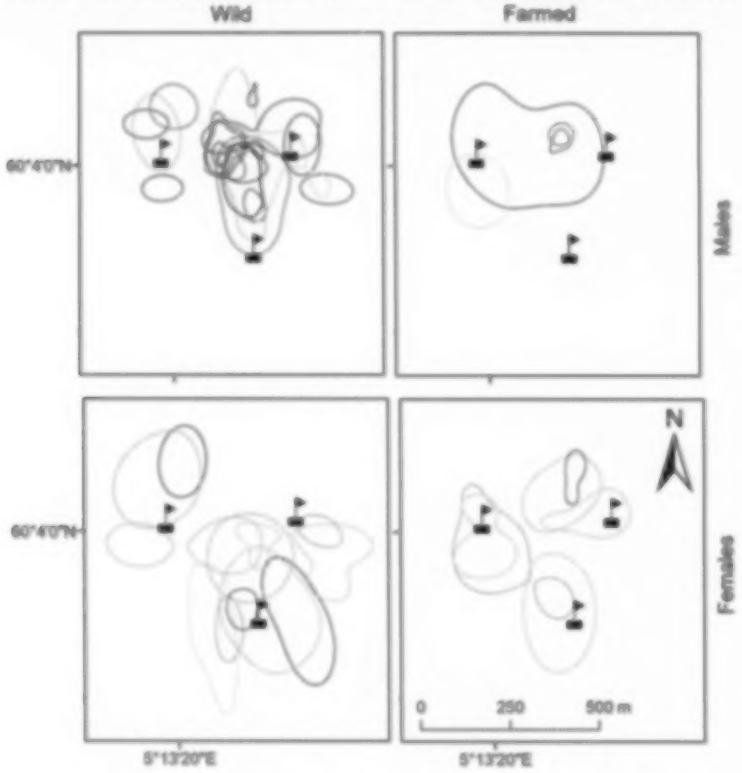


Fig. 3. Spatial overlap of all possible dyadic pairs of 28 fish (aggregate mean of individuals ± standard error, SE): (*a*) overlap indices of 50% (solid bars) and 95% (shaded bars) utilization distributions (home ranges) and (*b*) depth overlap (%).

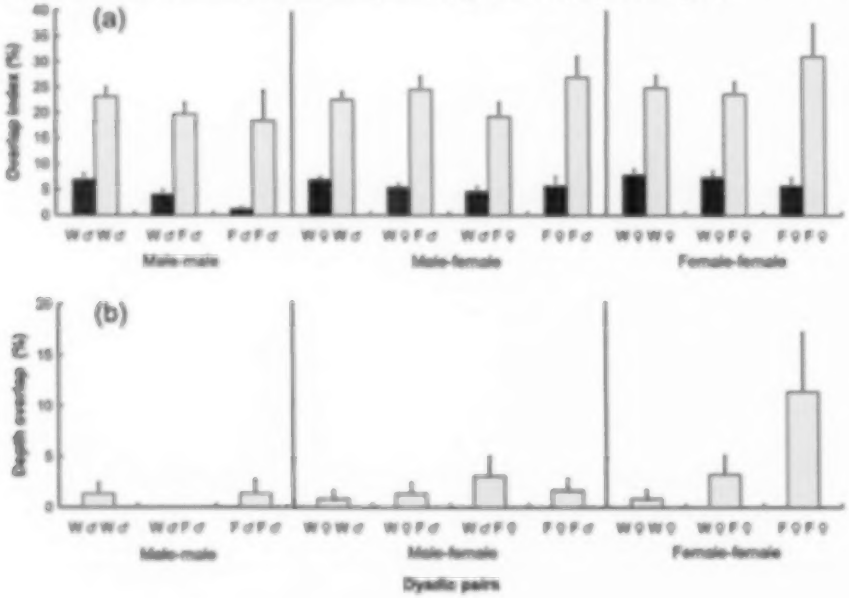
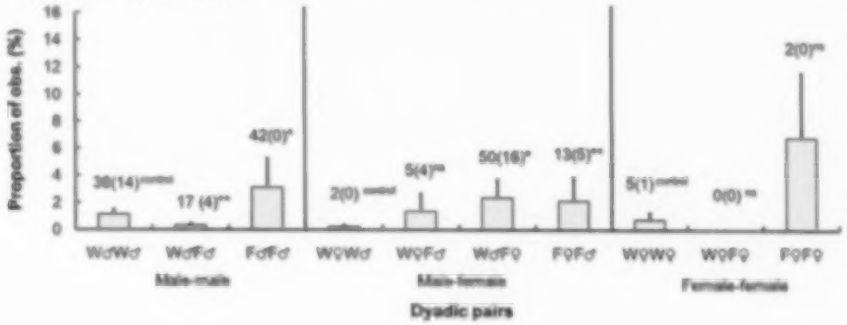


Fig. 4. Dyadic AS_{10} associations between 45 fish (12 wild ♂, 11 wild ♀, 11 farmed ♂, and 11 farmed ♀), given as the standardized mean percentage of observations ± standard error, SE. The number above each bar represents the total number of observed AS_{10}, with the total number of observed AS_5 in parentheses. The results of the a priori planned contrasts against wild groups (controls) are given in superscript (ns, not significant; **, $p \leq 0.01$; *, $p = 0.055$).



Spatial dynamics of females

Farmed females were over the spawning arena more often than wild females. In total, 67% of farmed ♀ positions (n = 2163) were over the spawning arena compared with 46% of wild ♀ positions (n = 4967). Female origin was significant in the LME model (G^2 = 4.2, df = 1, p = 0.04), with farmed females more likely to be positioned over the spawning arena than wild females (b = –1.2 ± 0.45, p = 0.009).

Spatial–temporal associations between individual fish

In total, 174 AS_{10} were observed, and 25% of these observations were at a scale of ≤5 m (i.e., 44 AS_5). The diel timing associations did not deviate significantly from random after correction for time in each diel period (G goodness-of-fit test = 0.39, df = 3, p = 0.72). The sex-origin type of dyads had a very strong effect on the likelihood of fish associating (G^2 = 1450.8, df = 9, $p < 0.001$). The fit of the model was improved by neither dyad mean swimming speed (G^2 = 0.32, df = 6, p = 0.57) nor an interaction between dyad swimming speed and association type (G^2 = 0.86, df = 5, p = 0.35).

Female–female associations were rare, with only 7 AS_{10} and 1 AS_5 observed (Fig. 4). The likelihood of female–female associations did not differ significantly between origin types (Fig. 4), and these associations involved only four wild and two farmed fish.

Male–male associations were frequent, with 97 AS_{10} and 18 AS_5 observed. Wild–wild and farmed–farmed associations were the most frequent. Over a third (37%) of wild male AS_{10} were within 5 m, whereas this was the case for none of the farmed male associations (Fig. 4). When standardized by the percentage of dyad sample size, associations (AS_{10}) between farmed and wild males were significantly less likely than the control (Fig. 4), whereas farmed–farmed associations were more likely (Fig. 4). Farmed ♂ – farmed ♂ associations involved only two fish (F♂206 and F♂182), but 11 fish were involved in wild ♂–♂ associations and 7 fish were involved in wild ♂ – farmed ♂ associations.

Male–female associations were frequent, with 70 AS_{10} and 25 AS_5 observed (Fig. 4). Wild ♂ – farmed ♀ associations were the most frequent with 50 associations, of which 32% were within ≤5 m. Standardised AS_{10} (percentage of dyad sample size) was significantly higher for farmed ♂ – farmed ♀ than the control (Fig. 4). The likelihood of wild ♂ – farmed ♀ associations also tended to be higher (b = 0.85 ± 0.45, p = 0.055) than the control (Fig. 4). Wild ♂ – farmed ♀ associations involved eight fish (4 wild ♂, 4 farmed ♀); farmed ♂ – farmed ♀ associations involved two females and three males; farmed ♂ – wild ♀ associations involved two males and two females, and wild ♂ – wild ♀ associations involved one female and two males.

In terms of repeated observations of associations between individual fish (Fig. 5), one farmed ♂ (F♂182) with a core usage area directly over the centre of the spawning area associated at least twice with six different fish (Fig. 5). Four fish associated at least twice with three different fish (Fig. 5). Several dyads associated on different days during the study, for example, dyad W♂9658 – F♀9656 associated on six days, and dyad F♂206 – F♂182 associated on 10 days.

All 97 male–male associations occurred either on or over the spawning arena. Two of seven female–female associations, two of five farmed ♂ – wild ♀ associations, and six of 50 farmed ♀ – wild ♂ associations occurred away from the spawning arena. Association depth was significantly affected by sex and origin (G^2 = 59.5, df = 7, $p < 0.001$, b = 1.2). Most fish associated with other fish at depths close to their mean depth range, but associations involving farmed females were closer to the seafloor and at the depth of the spawning arena (Fig. 6).

Discussion

Our results provide fine-scale field support for the contention that cod have a lek-like mating system (Hutchings et al. 1999; Nordeide and Folstad 2000; Windle and Rose 2006) and demonstrate that fish that have spent their entire lives in captivity can enter marine spawning shoals. Individual farmed cod had home ranges overlapping the central spawning arena, and the results indicate that hybridization between escaped farmed and wild fish is likely. This hybridization is likely to be biased towards farmed females, because farmed females regularly entered the spawning arena and were involved in most of the interactions with wild fish.

Fig. 5. Associations between individual fish with (*a*) coded transmitters and (*b*) continuous transmitters. Only associations that occurred more than once are included. The number in the centre of the circle corresponds to the individual tag number of each fish (shaded, farmed; open, wild), arrows indicate associations between fish, and the numbers adjacent indicate the number of AS_{10} associations (AS_5 is given in parentheses).

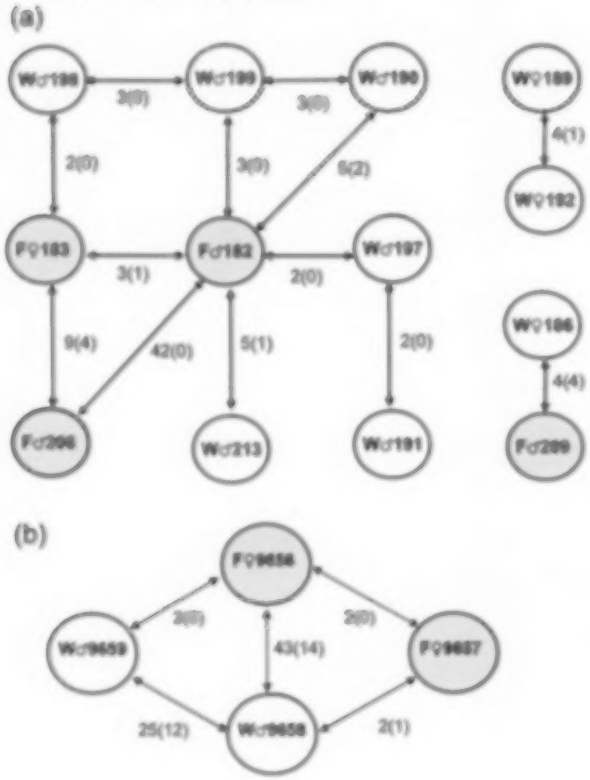
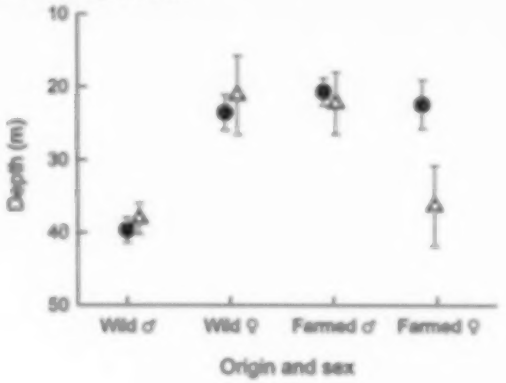


Fig. 6. The depth of fish–fish associations (AS_{10}): open triangles, mean depths (± standard error, SE) of associations; solid circles, overall mean depth (±SE).



The mating system: interactions between wild fish

Wild coastal cod maintained restricted home ranges on the spawning ground, as in earlier studies (e.g., Robichaud and Rose 2001; Windle and Rose 2006; Espeland et al. 2007), but we are aware of no other study that has compared home ranges between sexes in gadoids. In our study, wild males had small core home ranges that overlapped mostly in the centre of the study site, in an area that we term the "spawning arena", and to a lesser extent in a secondary area 150 m away. Wild females had a more dispersed and largely peripheral distribution, and a previous study showed that the wild females were pelagic, whereas the wild males were near the seafloor (Meager et al. 2009). Hence, in the present study, wild females were separated both vertically and horizontally from wild males. Such spatial separation between the sexes on a spawning ground is similar to that of other lekking fish species (McKaye 1983; Höglund and Alatalo 1995) and is supported by studies of the distribution of cod over larger spatial scales (Windle and Rose 2006).

Although not necessarily an obligatory feature of lekking systems (Höglund and Alatalo 1995), male defence of territories is demonstrated by cod in captivity (Brawn 1961; Hutchings et al. 1999). In our study, about half of the core home ranges of wild males were used exclusively, and core home range overlap between pairs was low. Overlap of 50% core home ranges has been used by other studies as a measure of territoriality and social organisation between males (e.g., Wronski 2005). In this context, although males tended to aggregate in the same area of our study site, they still had the potential to maintain territories, particularly when depth is also taken into account, because depth overlap was low and the average depth of wild males varied from 30 m to 47 m.

The likelihood of fish associating could partly be explained by their spatial distribution and predictions based on a mating lek. Wild males aggregated in a spawning arena and associated frequently. These associations may represent male–male agonistic interactions that have been well documented for cod in the laboratory (e.g., Brawn 1961; Hutchings et al. 1999; Rowe et al. 2008). The scarcity of female–female associations supports a lekking system and mirrors laboratory results that indicate that female interactions are infrequent in the mating system of cod (Brawn 1961; Hutchings et al. 1999).

According to the lekking hypothesis, females enter the male-dominated aggregation only when they are ready to spawn (Nordeide and Folstad 2000). The interval between spawning and the number of times that females spawn within a spawning season are dependent on factors such as female condition and water temperature, but we estimate a spawning interval of 3–4 days in our study (O. Kjesbu, Institute of Marine Research, N-5817 Bergen, Norway, personal communication, 2008). This implies that each female would not spawn more than 12 times over the 35-day study period. Hence, we would expect to observe only a small number of wild ♀ – wild ♂ associations, particularly when we consider the number of other potential mates in the spawning shoal that were not tracked and that spawning events and courtship sequences are likely to be short in duration (<3 min; Rakitin et al. 2001; J.E. Skjæraasen, unpublished data).

Were the associations reproductive behaviour?

The behaviour of individual fish towards each other is difficult to know for certain, because it is currently not feasible to visually observe the spawning behaviour of cod in the field. However, the patterns of dyad associations that we observed differed from random. The standardized rate of associations was strongly determined by fish sex and origin, and associations were much more frequent than would be expected based on the density of marked fish over the study area (approx. 1×10^{-6} fish·m^{-3}).

If we make the unrealistic assumption that the fish acted independent of one another, then the likelihood of random encounters between fish would be largely determined by their shared use of space and swimming speeds. However, our results show unequivocally that fish associations were not driven by these factors alone. Swimming speed was not statistically significant in our statistical model, and the group with the slowest swimming speed, wild males (J.J. Meager, unpublished data), had high rates of associations. Similarly, the group with the highest degree of volume overlap, farmed females, had only two associations. As a further example, the fish positioned the most frequently, W♀9651 (2743 positions), had a high degree of spatial overlap with other fish (mean UD_{95} = 24%) and yet was involved in no associations.

It might be argued that fish that had previously been kept together were simply shoaling after release, because wild fish were caught on the same spawning ground and farmed fish were from the same farm. It is doubtful that fish had the cognitive capacity to recognise all other individuals in the net pens where they were stored prior to release (Griffiths and Magurran 1997), but theoretically, they may have recognised each other by a shared characteristic such as odour (Ward et al. 2007). Nevertheless, associations between females of the same origin were rare, clearly indicating that prior recognition was not the only explanation for the associations observed in our study.

The ultrasound images indicated that all fish were within a week of spawning when they were released, and the movement of wild fish on this known spawning ground was similar to predictions inferred from a lek-like mating system. Further, five of the tracked fish (2 W♂, 1 F♂, 1 F♀, and 1 W♀) were later recaught and examined for macroscopic gonad stage, and all of these fish were either spent or spawning (Ø. Karlsen, Institute of Marine Research, N-5392 Storebø, Norway, unpublished data). Recently fertilized gadoid eggs were also present at the spawning ground during the study, and putative cod mating calls were recorded (J.E. Skjæraasen, unpublished data). In summary, the results strongly suggest that the fish that we released during the study spawned, and hence, the associations between fish were likely to have been mating interactions.

Interactions between farmed and wild fish

The spatial dynamics of farmed fish tended to be broadly similar to that of wild fish. For example, farmed males had smaller home ranges than farmed females, and the horizontal distributions of most farmed fish overlapped with the central spawning arena. As with wild fish, male–male associations were frequent and female–female associations were rare. However, farmed fish did tend to have smaller, less fragmented home ranges than their wild counterparts and utilized a smaller area of the spawning ground.

Although farmed males had low residency on the spawning ground and, hence, a small sample size (Meager et al. 2009), the core home ranges of the four fish analysed overlapped strongly with the spawning arena. They were, however, closer to the surface than the spawning arena (Meager et al. 2009) and therefore had very low depth–volume overlap with wild males and rarely associated with them. Two farmed males (F♂182, F♂206) that had small home ranges over the centre of the spawning arena were involved in most associations with wild males. The depth of associations involving these fish suggested that they encountered wild fish as they swam past, rather than by descending into the spawning arena. Although no associations involving these fish were observed within the spawning arena, it is difficult to determine if they were competitively excluded by wild fish or if they simply preferred to be closer to the surface.

The low residency of farmed males was one reason why farmed males rarely associated with wild females. Yet, all four associations between F♂209 and W♀186 occurred within a distance of 5 m, and in the laboratory, farmed males often courted wild females (Meager et al. 2009). We are therefore reluctant to dismiss entirely the risks imposed by farmed males in an actual escape, particularly when up to 160 000 cod have been reported to have escaped at once (Moe et al. 2007). Further, farmed males frequently associated with farmed females, suggesting spawning by pure farmed cod groups in the wild. Whether a natural spawning shoal is required to facilitate such behaviour is not known. Nevertheless, the potential of offspring of farmed fish to compete with local wild stocks already at low populations sizes suggests that this should be a priority for future research.

Farmed females frequently associated with wild males. Fifty associations involving eight different individual fish were observed, with repeated associations between individual dyads. Farmed females also spent more time over the spawning arena than wild females, and associations involving farmed females occurred at the depth of the spawning arena, on average 11 m deeper than their depth at other times. In the laboratory, farmed females readily hybridize with wild males (J.E. Skjæraasen, unpublished data). Together, these results indicate that escaped farmed females are likely to hybridize with wild populations and indicate that the risk of genetic introgression is likely to be biased towards farmed females, as with Atlantic and coho (*Oncorhynchus kisutch*) salmon (Fleming and Gross 1993; Fleming et al. 1996, 2000). Further, our results also suggest the potential for farmed females to interrupt the natural spawning system. The frequency at which farmed females were over the male spawning arena suggests that they were also present in the interval between spawning bouts. Large numbers of nonfertilizable females on the spawning arena may have energetic and mating opportunity costs to wild males (Kvarnemo and Ahnesjo 1996) or result in mate competition between wild females (Kvarnemo et al. 1995), but this should be the focus of further research.

In summary, our study provided new information about both the mating system of cod and the potential for escaped

farmed fish to interact and hybridize with wild marine fish. The spatial dynamics and associations between wild fish on the spawning ground were best described as a lekking mating system. The results also suggest that farmed cod that have spent their entire lives in captivity are likely to spawn in the marine environment and hybridize with their wild counterparts and that the potential for a sex bias in introgression can arise in the first generation of hatchery-produced fish.

There is a clear need for further studies investigating the genetic impacts of escaped farmed cod on localized cod populations. To this end, genetic approaches facilitate the inclusion of multiple spawning grounds and a longer time series. Our study also suggests the potential for farmed escapees to disrupt the reproductive behaviour of wild fish; hence, future studies should also consider behavioural interactions. Ultrasonic telemetry is costly and the number of animals that can be simultaneously tracked is limited by technological constraints, but it provides field behavioural data for cod that is currently unmatched by other technologies. Nevertheless, the results of the current study and other recent studies (e.g., Uglem et al. 2008; Meager et al. 2009) highlight the need for operational measures and technology to prevent farmed cod from escaping. The urgency for this is underscored by the fact that broodstock selection programmes are already underway in several countries and that 938 000 cod were reported to have escaped since 2004 in Norway alone (Norwegian Directorate of Fisheries 2009).

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Aquatic community metabolism response to municipal effluent inputs in rivers quantified using diel $\delta^{18}O$ values of dissolved oxygen

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Abstract: The spatial footprint over which municipal wastewater effluents cause changes to aquatic community structure and metabolism is key information required for the management of discharges into rivers. Longitudinal studies were undertaken on the Bow and South Saskatchewan rivers, Canada, to assess a new isotopic and modelling approach that combined O_2 and $\delta^{18}O$-O_2 diel (24 h) response curves to quantify changes in integrated community aquatic metabolism as a result of point-source wastewater inputs. Diel samplings were conducted over four seasons along 50 km transects at Calgary (Bow River) and Saskatoon (South Saskatchewan River). Diel O_2 and $\delta^{18}O$-O_2 cycles grew in magnitude downstream of effluent inputs in all seasons compared with upstream control sites. $\delta^{18}O$-O_2 depletions clearly revealed the stimulating effect of effluent on aquatic photosynthesis. Diel isotopic mass balance modelling showed community metabolic responses to effluent inputs were most pronounced in the spring and summer when photosynthesis and respiration rates were about two- to three-fold higher than at upstream control sites. Our findings revealed that sewage treatment plant nutrient additions resulted in an enhanced metabolic footprint that extended beyond 50 km downstream.

Résumé : Afin de gérer les rejets d'effluents municipaux d'eaux usées dans les rivières, il est essentiel de connaître l'étendue de l'empreinte spatiale laissée par les changements produits dans la structure et le métabolisme de la communauté aquatique. Nous avons entrepris des études longitudinales sur les rivières Bow et South Saskatchewan, Canada, pour évaluer une nouvelle méthodologie basée sur les isotopes et la modélisation qui combine les courbes journalières (24 h) de réponses de O_2 et de $\delta^{18}O$-O_2 afin de quantifier les changements dans le métabolisme intégré de la communauté aquatique à la suite d'apports d'eau usées provenant d'une source ponctuelle. Nous avons prélevé des échantillons sur 24 h au cours des quatre saisons le long de transects de 50 km à Calgary (rivière Bow) et à Saskatoon (rivière South Saskatchewan). La magnitude des cycles journaliers de O_2 et de $\delta^{18}O$-O_2 augmentent en aval des rejets d'effluents en toute saison par rapport aux sites témoins en amont. Les baisses de $\delta^{18}O$-O_2 montrent clairement l'effet stimulateur des effluents sur la photosynthèse aquatique. Une modélisation des bilans massiques isotopiques montre que les réponses métaboliques de la communauté aux rejets d'effluents sont plus prononcées au printemps et en été; à ce moment, les taux de photosynthèse et de respiration sont deux à trois fois plus élevés que dans les sites témoins en amont. Nos résultats indiquent que les additions de nutriments provenant des stations d'épuration des eaux usées produisent une empreinte métabolique accrue qui s'étend au-delà de 50 km en aval.

[Traduit par la Rédaction]

Introduction

Municipal sewage treatment plant (STP) effluent discharges into rivers can affect both water quality and the structure and function of the receiving aquatic ecosystems. STP nutrient enrichment of rivers stimulates aquatic primary productivity, potentially leading to degraded community structure and loss of function via eutrophication if the assimilative capacity of the receiving environment is exceeded (Chambers et al. 1997; Keeling 2005; Smith et al. 1999). Quantification of the environmental impact and spatial "footprint" of municipal STPs on rivers is complicated. Water column nutrient concentrations (various nitrogen and phosphorous forms) are most frequently used to monitor STP discharges and are often the minimum assay required for jurisdictional environmental monitoring regulations. Less frequently measured, both temporally and spatially, are the key biogeochemical and biological responses to nutrient additions. These include dissolved oxygen (O_2) demand and concentrations, chlorophyll *a*, and changes in phytoplankton and periphyton that are all linked to stimulated primary productivity (Carr et al. 2005*a*, 2005*b*; Kelly and Whitton

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1998). STP nutrient inputs and riverine responses are often nonlinearly correlated and are notoriously variable as a result of inter-related temporal factors (transient nutrient inputs, uptake rates, diel cycles, seasonality, plant and algal growth rates) and physical factors (water temperature and velocity, light, sampling location, substrate type, hydrologic mixing). Despite downstream dispersion and nutrient loss, the ecological and biogeochemical footprint of a single STP is not often considered as nutrients are recycled and primary organic matter is continuously generated and redeposited farther downstream. Additionally, many rivers have multiple point and non-point nutrient sources within their catchments, so assessing the overall ecological impact of a single STP may not be straightforward (Vandenberg et al. 2005). Thus, the development of new tools and approaches are needed to determine changes to whole-community metabolism in rivers resulting from anthropogenic nutrient inputs.

STP-derived nutrients discharged to rivers enhance primary productivity in the water column (phytoplankton) and on the substrate (periphyton, macrophytes), especially during the summer growing season, for 10s to 100s of kilometres downstream (Carr et al. 2005*b*; Scrimgeour and Chambers 2000). One key biogeochemical expression of aquatic photosynthesis (*P*) is that molecular O_2 is added to the water column by the photochemical oxidation of H_2O. As a result, dissolved O_2 has long been used to estimate *P* in aquatic systems (Falkowski and Raven 1997). *P* supplements the natural re-oxygenation via air–water gas exchange (*G*) on a diel basis. Concomitantly, enhanced *P* is accompanied by increased autotrophic respiration, as well as production and eventual oxidation of organic matter, stimulating heterotrophic respiration, which removes O_2 from the water column. Community respiration (*R*), the sum total of all O_2 consumption, has a rate that is primarily a function of water temperature and labile organic carbon availability (Baker et al. 2000). The problem of measuring and disentangling the three inter-related processes of *P*, *R*, and *G* has been longstanding (Lingeman and Vermij 1980; Chapra and Di Toro 1991).

Recently, the stable oxygen isotopic ratio ($\delta^{18}O$) of diel O_2 patterns has been proposed as an alternative method to quantify riverine aquatic *P*, *R*, and *G* rates under dynamic (e.g., 24 h diel changes) conditions (Parker et al. 2005; Tobias et al. 2007; Venkiteswaran et al. 2007). The benefit of dissolved O_2 isotopes is an additional natural tracer by which one can potentially measure whole-community metabolism, without having to rely on conventional light–dark bottle incubations or aquatic chamber experiments — methods that inherently bias results to the water column or the substrate. The diel $\delta^{18}O$-O_2 approach relies on the fact that key O_2 sources provide distinct isotopic tracers of origin (H_2O via *P*, atmospheric O_2 via *G*), whereas *R* simultaneously imposes reasonably well-known isotopic fractionation on O_2 consumption (Quay et al. 1995; Venkiteswaran et al. 2007). Hourly and diel changes in O_2 and $\delta^{18}O$-O_2 unfortunately negate the earlier use of simple steady-state oxygen isotopic models (Quay et al. 1995).

Although the dynamic $\delta^{18}O$-O_2 approach to studying riverine whole-community *P*, *R*, and *G* is robust in theory, extensive diel field testing and application to aquatic research is still limited (Parker et al. 2005; Tobias et al. 2007; Venkiteswaran et al. 2007). Here we test whether combined O_2 and $\delta^{18}O$-O_2 diel curves can be used to quantify whole aquatic community metabolism changes arising from point-source STP impacts located at upstream and downstream sites in the Saskatchewan River watershed, Canada (Bow River and South Saskatchewan River). We considered the effect of seasonality and spatial distance from STP source in an attempt to answer how much, when, and how far the impacts of nutrient additions have a measurable impact on the overall whole-community metabolism of the riverine receiving environment.

Materials and methods

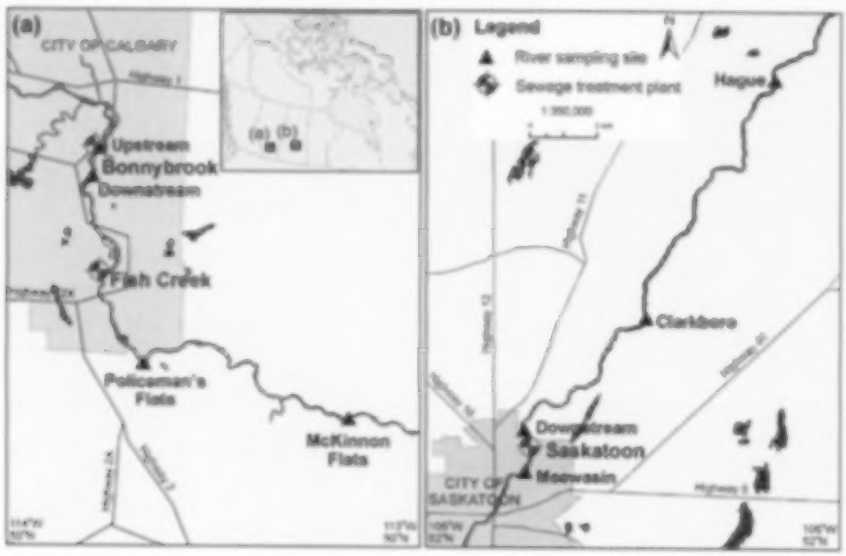
Study sites

Longitudinal transects over 50 km were established upstream and downstream of two major riverine point-source STPs in western Canada. The first transect was along the Bow River at the City of Calgary, Alberta (population 1.2 million; Fig. 1). The Bow River originates in the Rocky Mountains west of the city, with pristine, nutrient-poor waters derived from montane precipitation and snowmelt. The river flows through the City of Calgary where two advanced STPs discharge treated effluent directly into the Bow River. Bonnybrook STP is the major facility for the city, along with the smaller capacity Fish Creek STP. Nutrients added to the Bow River by these STPs are substantive. The upstream average concentration of nitrate is <0.2 mg $N{\cdot}L^{-1}$ (City of Calgary 2006), and the STPs discharge NO_3^- concentrations that range between 70 and 100 mg $N{\cdot}L^{-1}$ (Iwanyshyn et al. 2008). The upstream average total phosphorous (TP) concentration is <0.05 mg $\cdot L^{-1}$, the STP effluent averages around 0.6–0.8 mg $\cdot L^{-1}$, and TP varies around 0.03–0.04 mg $\cdot L^{-1}$ downstream of the city (City of Calgary 2002, 2006). The final treatment steps include UV irradiation and mechanical re-aeration before the effluent enters the Bow River via discharge conduits along the right bank. The effluent initially does not mix well with the river. Extensive macrophyte beds (mainly *Potamogeton* spp.) and increased periphyton were visible along the downstream effluent-plume side of the river. Groundwater inputs to the Bow River over the study area were not measured but are low (Grasby et al. 1999).

Four diel sampling stations were established: immediately upstream of the outfall (–0.1 km; right bank) of the Bonnybrook STP as the control, 3.2 km downstream of Bonnybrook STP (right bank), and at stations 24 km (right bank) and 47 km (left bank) downstream. Previous tracer studies show that the STP effluents are well mixed by ~25–50 km downstream (Iwanyshyn et al. 2008; Vandenberg et al. 2005). This longitudinal transect was ideal for examining the impact of a single urban STP source as the upstream watershed is pristine and has no significant point or cumulative non-point sources of nutrients. Site selection was controlled by road access to the river.

The second study site was a longitudinal transect on the South Saskatchewan River (SSR) at the City of Saskatoon (population 234 000; Fig. 1). The SSR is regulated by upstream dams, particularly the Gardiner Dam (Lake Diefenbaker) ~110 km upstream of Saskatoon. Diffuse, cumulative, non-point nutrient additions from western re-

Fig. 1. Location of sewage treatment facilities and seasonal diel riverine sampling sites on (*a*) the Bow River at Calgary, Alberta, and (*b*) the South Saskatchewan River at Saskatoon, Saskatchewan. Inset shows locations in Alberta and Saskatchewan, Canada.



gional agricultural activities are well established in the basin (Rock and Mayer 2006). Longitudinal transects on the SSR in 2004 showed that nitrogen concentrations generally decrease downstream from southern Alberta to below detection above Lake Diefenbaker. Nutrient concentrations in the outflow of Lake Diefenbaker to the SSR were higher than the lake's inflow and exhibited slight seasonal variations between 0.5 and 1.0 mg N·L^{-1} of NO_3^- (Nancy Glozier, Environment Canada, Water Quality Branch, 11 Innovation Boulevard, Saskatoon, Saskatchewan, unpublished data). No significant urban nutrient inputs occur between Lake Diefenbaker and Saskatoon. Saskatoon therefore also acts as a major single point-source nutrient input from its STP outfall. Background TP data for the SSR for the study period was unavailable, but the Saskatoon STP effluent averages ~0.4 mg·L^{-1} TP annually (McLeod et al. 2006). Effluent is discharged via diffusers fixed within the river bottom nearest to the left bank. Periphyton is visible and extensive below the STP at all downstream sites, consistent with extensive macrophyte (*Potamogeton* spp.) distributions prior to a mid-1990s tertiary STP upgrade (Carr and Chambers 1998). Four sampling stations were established: immediately upstream of the STP (~1.6 km, Meewasin) as the control, downstream of the STP (1.7 km, left bank), at Clarkboro (19 km, left bank), and at Hague (46 km, left bank). River access was controlled by road and ferry crossings and corresponded to those of a previous study (Carr and Chambers 1998). Groundwater fluxes to the SSR here are unknown but are believed to be low due to the highly impermeable nature of the underlying surficial glacial till (Keller et al. 1988).

For all stations on the Bow River and SSR, diel sampling was targeted to examine spatiotemporal aquatic metabolism responses to STP inputs under key hydrologic (Fig. 2) and temperature (Fig. 3) regimes in mid-summer (lower flow, high temperature, July 2004), early fall (base flow, cool temperature, October 2004), late winter under ice (low flow, cold temperature, March 2005), and late spring (high flow, warm temperature, May–June 2005). We conducted diel sampling for isotopic and O_2 data at all stations on each river within a 48 h period to avoid potential changes in weather and discharge that could affect metabolism dynamics and to ensure that all stations on each river were temporally comparable. Two field teams were deployed for the first 24 h at the two upstream sites and subsequently for 24 h at the two downstream sites. Weather forecasts were consulted to ensure full sunlight for the 48 h sampling. This insolation condition was met for all sampling times based on field photosynthetically active radiation (PAR) measurements (data not shown).

Regarding river flows, it was impossible to predict a priori the hydrologic conditions that would prevail over longer time scales. At diel time scales, water level changes of 5–20 cm in river depth over 24 h were observed on the SSR on all open-water dates because of upstream urban uptake and reservoir release, whereas on the Bow River, these open-water diel depth changes were only on the order of 10 cm. After the study, our sampling dates were compared with Water Survey of Canada river discharge and with the 2001–2007 mean discharges (Fig. 2). On the Bow River, river discharge on all sampling dates were close to the 7-year average; thus sampling was representative of mean flow conditions. On the SSR, where the river is regulated by upstream dams, discharge on two of the sampling dates was similar to the 7-year average. Discharge during the July 2004 sampling was significantly lower than the 7-year average and discharge was much higher during June 2005. Sampling dates on both rivers encompassed the seasonal temperature ranges (Fig. 3).

Fig. 2. Mean monthly river discharge on (*a*) the Bow River near Calgary and (*b*) the South Saskatchewan River near Saskatoon during the diel samplings in 2004 (shaded line and circles) and 2005 (continuous line and solid circles) compared with the mean monthly riverine discharge conditions (broken line) for 2000–2007. (All data were obtained from the Water Survey of Canada, http://www.ec.gc.ca/rhc-wsc/.)

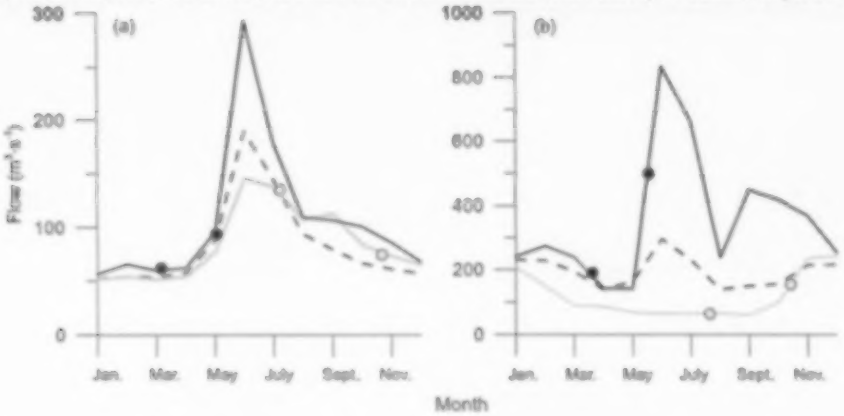
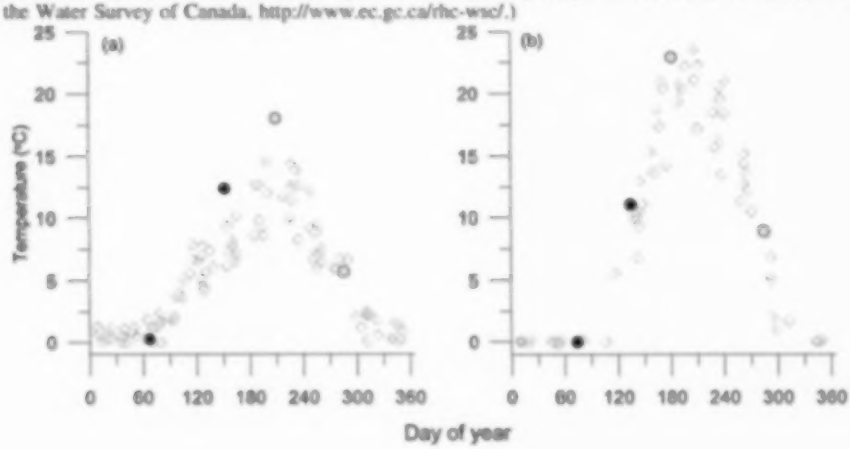


Fig. 3. Comparison of seasonal water temperatures in (*a*) the Bow River and (*b*) the South Saskatchewan River taken during the diel samplings in 2004 (shaded circles) and 2005 (solid circles) compared with mean daily temperatures for 2000–2007 (open diamonds). (All data were obtained from the Water Survey of Canada, http://www.ec.gc.ca/rhc-wsc/.)



Analytical procedures

At each sampling station, a deployable data sonde (Hydrolab DataSonde 4e or YSI 6000 series) was set up 3 m from the bank on the effluent side of the river using an anchored tripod fixed at river mid-depth. Data sondes were calibrated in the laboratory for conductivity and pH and on-site for O_2 and pressure (depth) prior to deployment. Sondes automatically logged temperature, O_2, O_2 saturation, conductivity, depth, and pH at 15 min intervals for 25 h. For comparative and modelling purposes, and to normalize for the large seasonal water temperature differences, all O_2 data are herein reported as percent saturation, corrected for local barometric pressure. River depths (0.6–1.1 m) and velocities (0.3–0.9 $m \cdot s^{-1}$) were measured at the beginning and end of each diel sampling (except for winter) using a metre stick and SonTek Acoustic Doppler Velocimeter. PAR was measured at three locations using a datalogger (LI-COR LI-1000; data not shown) for validating the light model used in the PoRGy model (Venkiteswaran et al. 2007).

To sample for $\delta^{18}O\text{-}H_2O$ and $\delta^{18}O\text{-}O_2$, a tube (1/4 inch HDPE plastic) was fastened to the sonde's protective cage adjacent to the sensors and routed to the riverbank. The line was fully purged with sample before collection. Samples for $\delta^{18}O\text{-}O_2$ were collected hourly in sterilized pre-evacuated, septum-capped 125 mL serum bottles to which 50 µL of saturated $HgCl_2$ had been added as a biocide. Serum bottles were allowed to fill via needle by suction (Wassenaar and Koehler 1999). At each station, water was collected for $\delta^{18}O\text{-}H_2O$ at the beginning and end of each diel sampling. Full diel samplings were completed in most cases; however, under winter ice cover, isotopic samples were not collected hourly or during the nighttime for logistical and safety reasons. One site on the SSR (DN-STP) was inaccessible in winter and spring, and sonde datalogging failed during the October 2004 sampling at this station. Similarly, sonde datalogging failed at the DN-STP site on the Bow River in March 2005.

In the lab, 5 mL of helium was added to each $\delta^{18}O\text{-}O_2$ se-

rum bottle to partition O_2 into a small headspace. Approximately 1–2 mL of the headspace gas, depending on the O_2 concentration in the water, was drawn into a 5 mL gas-tight syringe and injected into a continuous-flow isotope ratio mass spectrometry system as described previously (Wassenaar and Koehler 1999). Pure O_2 was used as the analysis gas and the isotopic reference gas. The $\delta^{18}O$-O_2 values were calculated by measurement of O_2 isotopes at 34/32 (m/z) on an isotope ratio mass spectrometer (Micromass Optima) and by comparison with a reference pulse of O_2. Sample repeatability (± standard deviation, SD) for $\delta^{18}O$-O_2 analysis sessions when corrected for source linearity and drift was better than ±0.2‰ (n = 20). Atmospheric $\delta^{18}O$-O_2 was assumed to be +23.5‰ with respect to Vienna Standard Mean Ocean Water (VSMOW) and was used as a single reference point to correct both sample and reference gas values. The $\delta^{18}O$-H_2O values were determined using standard methods (Kendall and Caldwell 1998). All $\delta^{18}O$-O_2 and $\delta^{18}O$-H_2O values are reported relative to VSMOW in the typical delta permil (δ‰) notation.

Isotopic modelling

The PoRGy dissolved oxygen isotope model (Venkiteswaran et al. 2007) was used to quantify P, R, and G using measured diel O_2 and $\delta^{18}O$-O_2 patterns. PoRGy is a graphical, user-friendly dynamic O_2 and $\delta^{18}O$-O_2 model that incorporates measured and assumed physical and biological covariates and isotope fractionation (http://www.science.uwaterloo.ca/~jjvenkit/PoRGy). A mass balance of O_2 and $\delta^{18}O$-O_2 is modelled through time, whereas P, R, and G are assessed at discreet time steps, akin to an isotopic version of the one-station O_2 models previously used in integrated estimates of whole-ecosystem metabolism (Hornberger and Kelly 1975; O'Connor and Di Toro 1970; Odum 1956). A key improvement of PoRGy is the addition of a second equation to account for the stable isotopic composition of dissolved O_2. A detailed discussion of the effect of each of the covariates (P, R, gas exchange coefficient (k), isotopic fractionation factor (α_R), temperature) on diel O_2 and $\delta^{18}O$-O_2 curves was outlined previously (Venkiteswaran et al. 2008). As a result of the different effects of these variables on O_2 and $\delta^{18}O$-O_2, PoRGy can be used to find combinations of P, R, k, and α_R that best fit observed field data. The original PoRGy model was ported to MATLAB 7.6.0 (The MathWorks, Inc., Natick, Massachusetts; http://www.mathworks.com) to enable automated iterative curve-fitting using measured field covariates (O_2, $\delta^{18}O$-H_2O, $\delta^{18}O$-O_2, temperature, time, date, location) and constrained unknown covariates (metabolic rates, α_R, k). Unknown covariates were constrained within the model based on reasonable literature values. For example, metabolic rates (expressed as fluxes) were assumed to be above 0 mg $O_2 \cdot m^{-2} \cdot h^{-1}$ but were not likely to exceed 5000 mg $O_2 \cdot m^{-2} \cdot h^{-1}$. The value of α_R (where isotope fractionation factors are defined as the rate of reaction of the heavy isotopologue to that of the light isotopologue and are typically <1) was constrained based on literature values between 1.000 and 0.975 (Venkiteswaran et al. 2007). Given the much greater uncertainty in k than for all other covariates (Jha et al. 2004), a range of three orders of magnitude of k was allowed, from 0.001 to 1 $m \cdot h^{-1}$. PoRGy is similar to the exact inverse solution method proposed by Tobias et al. (2007); both approaches use differential equations of O_2 and $\delta^{18}O$-O_2 with time to solve for a solution that best fits the observed field data.

Beginning with randomized starting points within field-measured and assumed constraints, the Matlab "fminsearch" function was used to seek a combination of P, R, k, and α_R that minimized the combined sum of squared errors between observed field data (O_2 and $\delta^{18}O$-O_2) and modelled data (O_2 and $\delta^{18}O$-O_2). To compare model results with our field site data, goodness-of-fit r^2 values were calculated by least squares regressions of field data versus model results. Each site–date combination model was run 20 times, and the first 10 results having $r^2 > 0.5$ were selected for averaging as possible model solutions. In some instances where combined O_2 and $\delta^{18}O$-O_2 data were sparse (e.g., winter), or where an irresolvable diel pattern existed, the PoRGy model was not able to find a model solution with $r^2 > 0.5$, so these model results are not reported.

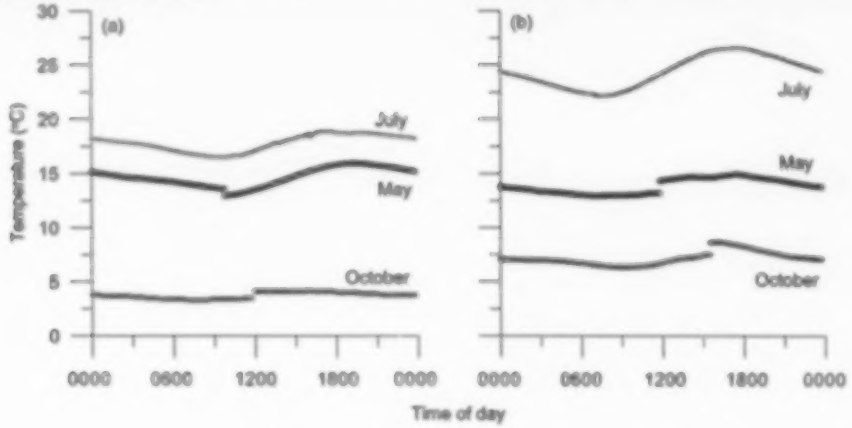
Results and discussion

Seasonal and diel fluctuations

Temperature places crucial controls on biological activity rates, as well as on O_2 solubility in natural waters. River temperature and discharge for the Bow River and SSR were summarized and compared with the 2000–2007 means (Figs. 2 and 3). For both rivers, seasonal river warming began after ice break-up, between days 80 and 120. Daily mean temperatures peaked near day 200 and declined thereafter until freeze-up, around day 350 (Fig. 3). Maximum ice thickness during winter sampling (March 2005) ranged from a few centimetres with occasional upstream open leads (Bow River) to ~75–100 cm (SSR). Maximum summer temperatures were around 18 °C in the Bow River and 24 °C in the SSR. Temperature trends on both rivers were similar to their 2000–2007 means, with the exception of the July 2004 sampling on the Bow River when the river temperature was about 5 °C warmer than the average. All sites exhibited smaller degrees of diel temperature fluctuations dependent on daily insolation (Fig. 4). The largest diel temperature change occurred during the summer: a 2.5 °C range on the Bow River and a 5 °C range on the SSR. For all other seasons, the diel temperature ranges were small (May and Oct) to nonexistent in winter (constant temperature of 0.1 °C, data not shown). Specific conductivity showed no diel patterns, and pH yielded a weak diel response in summer only (data not shown).

Flow velocity and river depth affect G (via k) and may disturb substrate biota (e.g., scouring). Our objective to sample under "typical" river discharge conditions was largely met for the Bow River (Fig. 2). However, discharge on the SSR was nearly twice the average during the May 2004 sampling but was about half the average during the July 2004 sampling (Fig. 2). Although discharge on the SSR was not "typical" for the entire study period, flow velocities were not affected as much as river depth. Because k controls the maximum and minimum O_2 concentrations through the relationship $k = G/Z$, where Z is river depth, and because P and R are areal rates, it follows that river depth affects the magnitude of diel swings. Thus, rivers should not be compared on the basis of O_2 curves

Fig. 4. Example of diel water temperatures in the Bow and South Saskatchewan rivers for the May through October samplings. In winter, the water temperature is +0.1 °C at all sites.



alone — accurate whole-stream metabolic comparisons require the modelling of *P*, *R*, and *G*.

O_2 and $\delta^{18}O$-O_2 response to STP effluents

Control sites

The results of diel O_2 and $\delta^{18}O$-O_2 sampling for each longitudinal STP transect over four seasons are summarized (Figs. 5 and 6). Several qualitative and comparative observations about community metabolic responses to STP effluent inputs could be made. At the control site (Bonnybrook) on the Bow River (Fig. 5, upper left panel), O_2 was predominantly undersaturated (<100% saturation, range of ~80%–110%) over all seasons, with lowest O_2 saturation occurring in winter under ice and just before sunrise in the spring, summer, and fall. The metabolic status of the control site reflects ambient processes impacting the river between 13 and 30 km upstream (see Other modelling considerations) as the river passes through the City of Calgary. Diel O_2 ranges were weakest in the spring and strongest in the summer, exceeding 100% oxygen saturation by mid-afternoon in the summer. Similarly for the SSR (Fig. 6, upper left panel), O_2 at the upstream control site (Meewasin) was nearly 100% saturated across most seasons, generally with slightly smaller diel O_2 cycles than observed in the Bow River. In July, however, there was a larger diel O_2 pattern: the lowest O_2 saturation occurred before sunrise and the greatest O_2 saturation occurred by mid-afternoon, similar to the summer Bow River control site.

These predominantly undersaturated O_2 conditions at the upstream control sites suggested that these rivers upstream of their STP effluent inputs were respiration-dominated, i.e., *R* exceeded *P* and *G*. However, the $\delta^{18}O$-O_2 data provided additional insight into the controlling processes (Figs. 5, 6, lower left panel). If isotopic fractionation were due to *R* alone, it would result in $\delta^{18}O$-O_2 values *greater* than +24.2‰ (the air-equilibrium value) in the absence of *P*. It was noteworthy that $\delta^{18}O$-O_2 values at the control sites exhibited a large isotopic range, mostly lower than +24.2‰ and as low as ~+15‰. The lowest $\delta^{18}O$-O_2 values corresponded to the highest O_2 saturation values per seasonal diel cycle, revealing a sensitive isotopic response to the diel input of a small amount of O_2 from *P*. These O_2 and $\delta^{18}O$-O_2 patterns helped to establish the baseline metabolic and *G* rates for these rivers prior to STP effluent inputs (see PoRGy modelling below).

Downstream STP impacts

The aquatic productivity response to STP effluent inputs was manifested seasonally and spatially as progressive increases in diel O_2 and $\delta^{18}O$-O_2 fluctuations downstream (Figs. 5, 6). In the Bow River below the STP, progressively larger diel fluctuations in O_2 and $\delta^{18}O$-O_2 values were observed downstream, particularly in the summertime when the greatest insolation and warmest water occurred (Fig. 5). In part, because the solubility of O_2 is negatively correlated with temperature, summer O_2 and $\delta^{18}O$-O_2 diel fluctuations were more pronounced than during colder conditions. The daily range of O_2 saturation downstream of the Bow STP was significantly larger than at the control site, from nighttime lows of ~60% saturation to mid-afternoon highs up to ~140% in summer. The O_2 and $\delta^{18}O$-O_2 were highly correlated (r^2 = 0.75 to 0.95; Figs. 7, 8) in the largest summertime diel fluctuations, with the lowest $\delta^{18}O$-O_2 values (as low as +11‰, higher *P* rates) at mid-afternoon and the highest $\delta^{18}O$-O_2 values (up to +26‰, higher *R*) at dawn (Figs. 5, 6). Average O_2 saturation levels increased downstream of the STP (Table 1), showing the importance of increased *P* resulting from the nutrient additions.

Below the Saskatoon STP, similar spatiotemporal O_2 and $\delta^{18}O$-O_2 fluctuations were observed (Fig. 6). The largest diel swings occurred in summer at sites most distal from the STP effluent input. The largest diel fluctuation occurred at Hague (~46 km below the Saskatoon STP), with daily ranges of O_2 saturation of 60%–140% and $\delta^{18}O$-O_2 of +8‰ to +22‰. Average O_2 also increased downstream of the STP over the entire 50 km river reach. Because river morphology and flow velocity did not change appreciably over the two longitudinal transects on the Bow River or SSR, it was clear that the impact of STPs on whole-river metabolism exceeded 50 km and likely extends much further downstream.

The size, shape, and location of diel data on an O_2 vs.

Fig. 5. Seasonal and longitudinal diel O_2 (% saturation (SAT)) and $\delta^{18}O\text{-}O_2$ fluctuations in the Bow River from above the sewage treatment plant (STP) (–0.1 km) to 47 km downstream of the effluent inputs. The Calgary Bonnybrook STP discharges effluents at km 0. ASW, air-saturated water. Symbols: squares, 7–8 March 2005; circles, 30–31 May 2005; plus signs, 20–21 July 2004; diamonds, 19–20 October 2004.

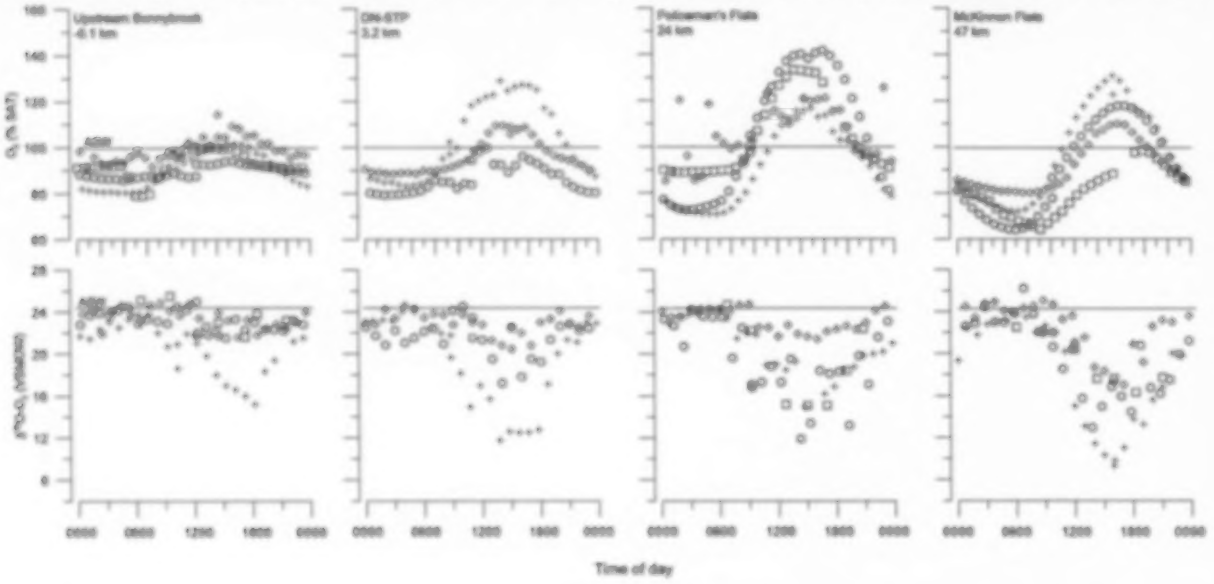
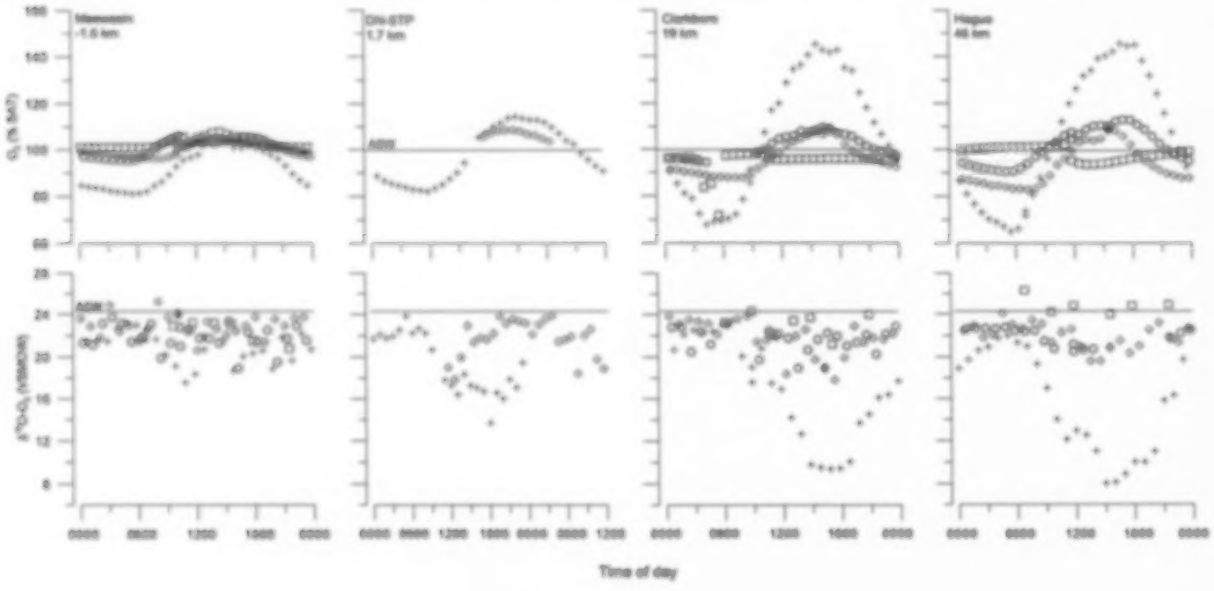


Fig. 6. Seasonal and longitudinal diel O_2 (% saturation (SAT)) and $\delta^{18}O\text{-}O_2$ fluctuations in the South Saskatchewan River from above the sewage treatment plant (STP) (–1.6 km) to 46 km downstream of the effluent input. The Saskatoon STP discharges at km 0. ASW, air-saturated water. Symbols: squares, 15–16 March 2005; circles, 24–25 May 2005; plus signs, 15–16 July 2004; diamonds, 14–15 October 2004.



$\delta^{18}O\text{-}O_2$ cross plot is controlled by the interplay of *P*, *R*, and *G*, and although informative in a relative and visual sense, PoRGy modelling of the data is required to obtain quantitative information because of the confounding effects of variable metabolic rates and differences in *k* and temperature between dates and sites (Figs. 7, 8). As expected, diel data clustered near air-saturation conditions for the control sites upstream of the STP effluent outfalls. Longitudinally, samples closest to air-saturation conditions were the wintertime samples, with progressively increasing displacements for fall, spring, and summer, indicating increasing metabolic activity through those seasons. Clearly, the more productive a

Fig. 7. Cross plot of O_2 (% saturation) versus $\delta^{18}O\text{-}O_2$ for seasonally conducted diel collections on a longitudinal transect for the Bow River. Sewage treatment plant (STP) effluent input from the City of Calgary Bonnybrook STP occurs at km 0. Solid circle denotes air-saturated water (100% saturation, $\delta^{18}O\text{-}O_2$ = +24.2‰). Symbols: squares, 7–8 March 2005; circles, 30–31 May 2005; plus signs, 20–21 July 2004; diamonds, 19–20 October 2004. Continuous line is least squares regression through the summertime diels.

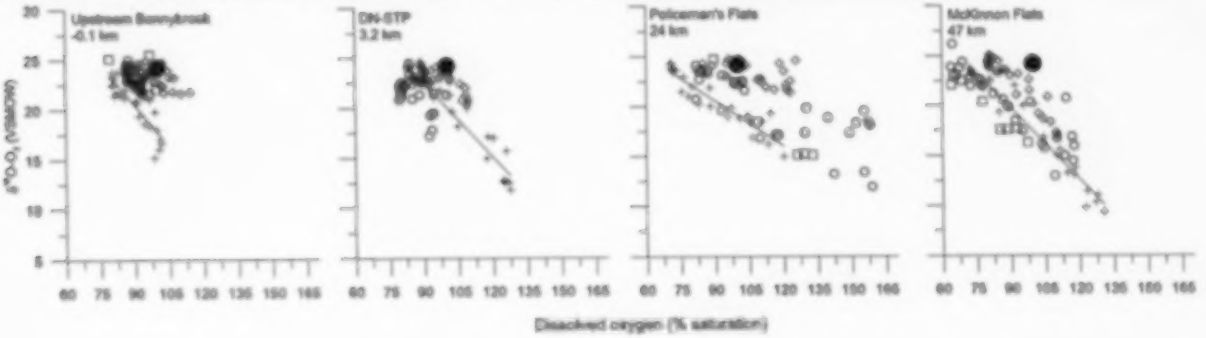
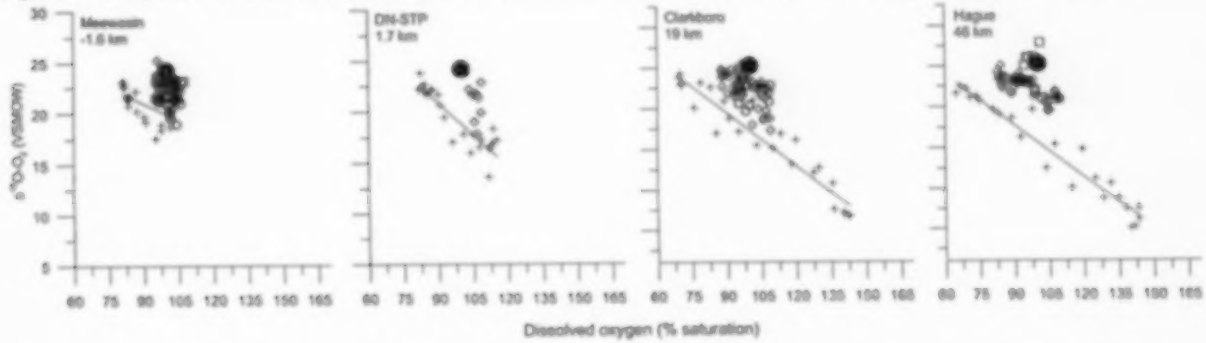


Fig. 8. Cross plot of dissolved oxygen (% saturation) versus $\delta^{18}O\text{-}O_2$ for seasonally conducted diel collections on a longitudinal transect for the South Saskatchewan River. Sewage treatment plant (STP) effluent input from the City of Saskatoon STP occurs at km 0. Solid circle denotes air-saturated water (100% saturation, $\delta^{18}O\text{-}O_2$ = +24.2‰). Symbols: squares, 15–16 March 2005; circles, 24–25 May 2005; plus signs, 15–16 July 2004; diamonds, 14–15 October 2004. Continuous line is least squares regression through the summertime diels.



river becomes (flow conditions and k being equal), the larger the diel swings become, and the further to the lower left of the cross plot the diel data will lay. Hence these types of plots provide a qualitative and easily grasped picture of metabolic status, all other factors being equal (depth, flow, etc.).

Quantifying of *P*, *R*, and *G* in response to STPs

The PoRGy dissolved oxygen isotope model (Venkiteswaran et al. 2007) was used to quantify P, R, and G at all sites where full diel patterns were measured (Tables 1, 2; Figs. 9, 10). Of the 29 site-date combinations measured on the Bow River and SSR, six were not successfully modelled (Tables 1, 2). Five of these were on the SSR during the winter and were not successfully modelled primarily due to the lack of sufficient temporal diel resolution in the data (see sampling issues noted in Materials and methods). The other was where the measured diel patterns were not explainable mainly by P, R, and G (i.e., some other unknown factors such as temporal changes in STP effluent quality), and the diel curve did not have the characteristic sinusoidal shape (Venkiteswaran et al. 2008). Of the 23 diel data sets that were successfully modelled, r^2 values were typically greater than 0.75 for field versus modelled O_2 saturation, with only eight lower than that. In general, O_2 saturation r^2 values were greater than those for $\delta^{18}O\text{-}O_2$ (Tables 1, 2). This was also noted in all but one of previously published PoRGy model fits (Venkiteswaran et al. 2007, 2008). In cases where the r^2 was <0.85 for field versus modelled $\delta^{18}O\text{-}O_2$, the PoRGy model fits tended to deviate the most from observed field data, either at mid-day or in the overall general sinusoidal shape. This suggested that there may be additional factors at play, or that some covariate rates vary over a diel time frame. PoRGy uses average daily values (maximum P rate (P_{max}), R rate at 20 °C (R_{20}), k, and α_R) for the entire diel period. If R_{20} or α_R are not constant over 24 h, or changes occurred in the hydrologic mixing of the plume in the river at sites proximal to the STP, then the PoRGy model fits may deviate from observed data (also useful information). Although the use of averaged rates are an acknowledged limitation to the PoRGy oxygen isotope modelling, it was noteworthy that well over 75% of the aquatic productivity variance was explainable by the interplay between P, R, and G (cf. Venkiteswaran et al. 2007).

Productivity responses to STP effluent — Bow River

PoRGy modelled P and R rates in the Bow River (Fig. 9; Table 1) markedly increased below the upstream control as a result of STP inputs. P rates in May and July increased

Table 1. Field variables and PoRGy model results for the seasonal and longitudinal transects on the Bow River.

	Bonnybrook (–0.1 km)				DN-STP Bonnybrook (3.2 km)		
Variables	20 July 2004	20 October 2004	7 March 2005	1 June 2005	20 July 2004	20 October 2004	1 June 2005
Known variables							
$\delta^{18}O$-H_2O (‰)	–19.2	–18.6	–18.7	–18.8	–19.3	–18.9	–19.3
Latitude (°N)	51.010	51.010	51.010	51.010	50.986	50.986	50.986
Longitude (°W)	114.018	114.018	114.018	114.018	114.026	114.026	114.026
Altitude (m above sea level)	1025	1025	1025	1025	1018	1018	1018
Day of year	202	294	66	152	202	294	152
Year (CE)	2004	2004	2005	2005	2004	2004	2005
Input variables for model fit							
P_{max} (mg·m^{-2}·h^{-1})	559	844	1090	135	2161	1921	1152
R_{20} (mg·m^{-2}·h^{-1})	337	170	692	37	503	554	535
k (m·h^{-1})	0.173	0.085	0.124	0.070	0.397	0.297	0.376
α_R	0.999	0.976	0.979	0.976	0.996	0.991	0.993
Calculations and model fit							
P:R:G	0.91:1.85:1	1.24:1.48:1	0.80:1.80:1	1.54:1.13:1	1.16:0.92:1	0.71:1.32:1	1.12:1.42:1
P:R	0.49:1	0.84:1	0.45:1	1.36:1	1.26:1	0.54:1	0.79:1
P (mg O_2·m^{-2}·h^{-1})	145	70	124	36	559	161	309
R (mg O_2·m^{-2}·h^{-1})	295	84	276	27	444	298	394
G^* (mg O_2·m^{-2}·h^{-1})	159	57	153	24	481	226	279
r^2 (saturation)	0.97	0.80	0.60	0.85	0.98	0.97	0.78
r^2 (isotopes)	0.76	0.36	0.54	0.29	0.93	0.64	0.23

Note: The kilometre value in parentheses after the transect name represents the distance above or below the Calgary Bonnybrook STP. G^* is gross G, i.e.,

from the control site (35–120 mg O_2·m^{-2}·h^{-1}) to the first site downstream of the STP (to a maximum of 550–560 mg O_2·m^{-2}·h^{-1}). There were small declines in the P rate in October downstream of the STP in the Bow River (Table 1). R rates increased in all seasons downstream of the Calgary STPs (to a maximum of 440 mg O_2·m^{-2}·h^{-1}). However, R rates declined to values similar to the upstream control site by about 22 km downstream (e.g., Policeman's Flats). R rates also exhibited seasonal differences and, not surprisingly, were greatest in summer and lowest in winter, revealing the expected positive relationship between water temperature and community R rates.

For gas exchange, the Bow River k values varied by more than fourfold. In all seasons, k was highest immediately downstream of the Bonnybrook STP compared with the control site, suggesting that some other factors were affecting gas exchange. There was nothing notable in the river velocity, width, depth, or substrate to indicate a major difference in k over such a short distance (<3 km). However, the STP effluent undergoes UV irradiation with mechanical re-aeration immediately before release into the discharge channel that enters along the bank of the Bow River. Increased turbulence in this channel was also directly observable as river surface disturbance, surging, eddies, and frothing. Because the STP plume initially does not mix well with the rest of the river, the plume may have retained some of its "upstream" mechanical and discharge re-aeration history from the STP facility, which was easily detectable using the $\delta^{18}O$-O_2 patterns in the river.

The *P:R:G* ratio is much better than the conventional *P:R* ratio at describing the vulnerability of an aquatic ecosystem to external stressors because it fully takes into consideration how much re-aeration occurs to attenuate the potential extremes caused by enhanced aquatic metabolism (Venkiteswaran et al. 2008), e.g., O_2 undersaturation to levels that affect aquatic life. The P and R rates along the Bow River longitudinal transect were never more than twice, or less than half, of G (0.91:1.9:1 and 1.2:0.5:1), which suggested that re-aeration rates in the Bow River are sufficiently high to moderate the current increased levels of aquatic productivity (P) resulting from municipal STP nutrient inputs to the river. There was no apparent longitudinal or seasonal trends in *P:R:G* ratios on the Bow River as the similar downstream and seasonal effects exhibited by P and R rates were compensated for by the changes in k (Fig. 10).

Productivity responses to STP effluent — South Saskatchewan River

In the SSR (Fig. 10; Table 2), P was lowest (140–200 mg O_2·m^{-2}·h^{-1}) at the control site upstream of the Saskatoon STP. In March and July, P increased downstream of the Saskatoon STP to a maximum of 420–430 mg O_2·m^{-2}·h^{-1}, whereas there was no discernible change in P downstream of the STP in October or May. The R rates were generally lowest above the Saskatoon STP and increased downstream. The longitudinal increase in R was observed over all four seasons. Compared seasonally, R in the SSR was highest in the summer and lowest in the winter, similar to the Bow River, which again suggested that aquatic R was linked to water temperature (cf. Wetzel 2001) and is greater in the summer. It was unclear whether the apparent decline in R (and low P) in July at the station below the SSR STP was an artefact of inhibitory effects of the STP outfall (e.g., from effluent chlorination). In the SSR, k val-

Policeman's Flats (24 km)			McKinnon Flats (47 km)			
21 July 2004	7 March 2005	31 May 2005	21 July 2004	19 October 2004	7 March 2005	31 May 2005
–19.5	–18.7	–19.0	–19.7	–18.8	–18.9	–18.6
50.845	50.845	50.845	50.805	50.805	50.805	50.805
113.951	113.951	113.951	113.696	113.696	113.696	113.696
978	978	978	937	937	937	937
203	66	151	203	293	66	151
2004	2005	2005	2004	2004	2005	2005
733	1792	1862	787	1212	641	1157
319	305	295	250	394	240	697
0.120	0.117	0.185	0.091	0.079	0.005	0.082
0.990	0.985	0.975	0.990	0.987	0.975	0.980
1.18:1.76:1	1.24:0.80:1	1.17:0.52:1	1.55:1.73:1	0.98:1.76:1	8.32:11.47:1	1.58:1.49:1
0.67:1	1.54:1	2.23:1	0.90:1	0.56:1	0.72:1	1.06:1
189	204	498	202	104	73	309
282	132	224	225	187	101	293
160	165	427	130	107	9	196
0.98	0.99	0.97	0.98	0.99	0.97	0.98
0.87	0.97	0.62	0.91	0.88	0.90	0.81

the sum of the influx and efflux, not their difference.

ues varied little seasonally and longitudinally, despite the apparent changes in discharge (Fig. 2). The k values ranged between 0.12 and 0.24 m·h^{-1}. These rates were well within the range predicted based on physical river and flow parameters used by the Owens, Churchill, and O'Connor equations (Jha et al. 2004). Because the effluent was discharged into the SSR via in situ diffusers, we did not observe the artificial re-aeration imprint observed on the Bow river below the Bonnybrook STP.

Overall, the P and R rates for the Bow River and SSR were mostly similar, despite large differences both in nutrient loading (e.g., differences in population of Calgary versus Saskatoon) and in the amount of STP discharge. However, the SSR receives more nutrients from non-point-source agricultural activities upstream compared with the Bow River. The P:R:G ratios in the SSR were generally >1:>1:1 (Table 2), revealing that aquatic metabolism was the greater driver of O_2 dynamics than re-aeration. However, because the greatest ratios, those deviating most from unity, were only 1.2:2.0:1 and 2.0:1.7:1, this suggested that the resulting increase in diel O_2 curves were also greatly dampened by gas exchange. The P:R:G ratios in the SSR varied less than those in the Bow River.

Other modelling considerations

Given that water moving along a fixed sampling point in the river is integrating 24 h of upstream processes and flow, a question may be asked about how far upstream this spatial "diel window" extends. Clearly, point-source metabolic and G effects on O_2 and $\delta^{18}O$-O_2 in rivers can only be exhibited for a finite distance downstream. This diel window is controlled by k and mean river water velocity (v), assuming that river discharge and depth are relatively constant over the river reach and over the diel period. The upstream distance over which estimates of metabolism and gas exchange are exponentially integrated may be estimated by a first-order relationship in which $3v$-k^{-1} describes the distance over which 5% of an upstream gas load remains in the river at the sampling point (Chapra and Di Toro 1991). For the Bow River, this diel window ranged between 13 and 31 km, which is about 50% of that suggested by the average daily travel distance of the river based on v. In the SSR, this diel window ranged between 15 and 22 km, which is less than or about equal to the average daily travel distance of the river. Hence, the transect spacing used in this study was appropriate for detecting changes in metabolism along the rivers.

For isotopic fractionation, the best-fit PoRGy modelled values of α_R were 0.985 ± 0.005 (n = 14) in the Bow River and 0.994 ± 0.005 (n = 9) in the SSR. These α_R values were within previously published ranges for O_2 isotopic fractionation (Kiddon et al. 1993; Lehmann et al. 2009; Quay et al. 1995). There were no correlations between α_R and other model parameters such as P and R rates, descriptive values such as the two r^2 values, or with season or location relative to STPs. These results, combined with the knowledge that α_R affects only the vertical translation of $\delta^{18}O$-O_2 values (Venkiteswaran et al. 2008), suggested that α_R was a unique parameter whose best-fit value affected the ability of PoRGy to reproduce field data. Using the July data at Hague on the SSR as an example of where the best-fit α_R value was 0.996, the effect of α_R can be assessed. If α_R were 0.986 (greater isotopic fractionation), a difference of 10‰, the best-fit P and R rates would have been 3% lower, and k would have been 25% lower. The mean O_2 and $\delta^{18}O$-O_2 values of the field data and best-fit were 105% and 15.5‰ and 106% and

Fig. 9. Selected example diel field data (solid circles) and PoRGy model fits (shaded lines) data from (*a*) DN-STP Saskatoon, 13 July 2004, (*b*) Policeman's Flats, 7 March 2004, and (*c*) McKinnon Flats, 31 May 2005. The original frequency of O_2 saturation data was reduced to match the $\delta^{18}O$-O_2 data. Equilibrium air–water saturation shown as dotted lines in the diel figures and air-saturated water (ASW) is shown as an open circle in the cross plots. All other model fits are tabulated in Table 1.

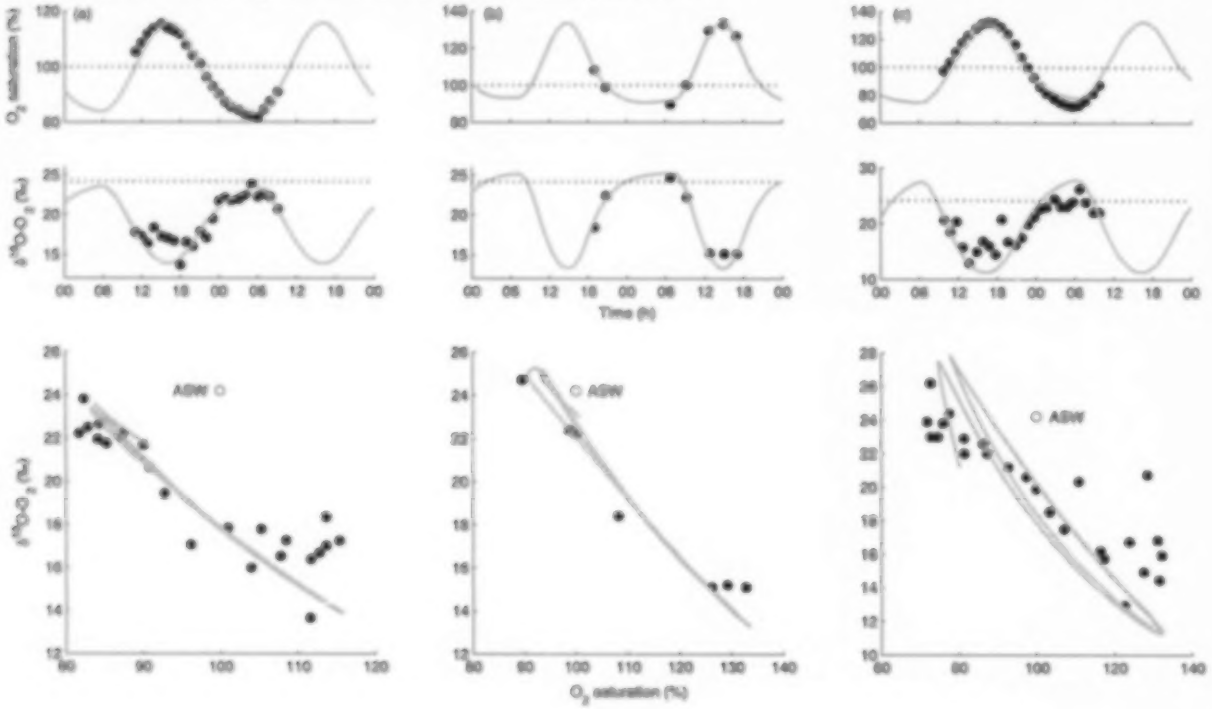


Fig. 10. Photosynthesis (*P*), respiration (*R*), and gas exchange *k* values on (*a*) the Bow River and (*b*) the South Saskatchewan River as a function of distance downstream from the sewage treatment plant (STP) outfalls in July 2004 (circles), October 2004 (squares), March 2005 (shaded ×), and May 2005 (shaded squares). The first data (<0 km) are the upstream control sites.

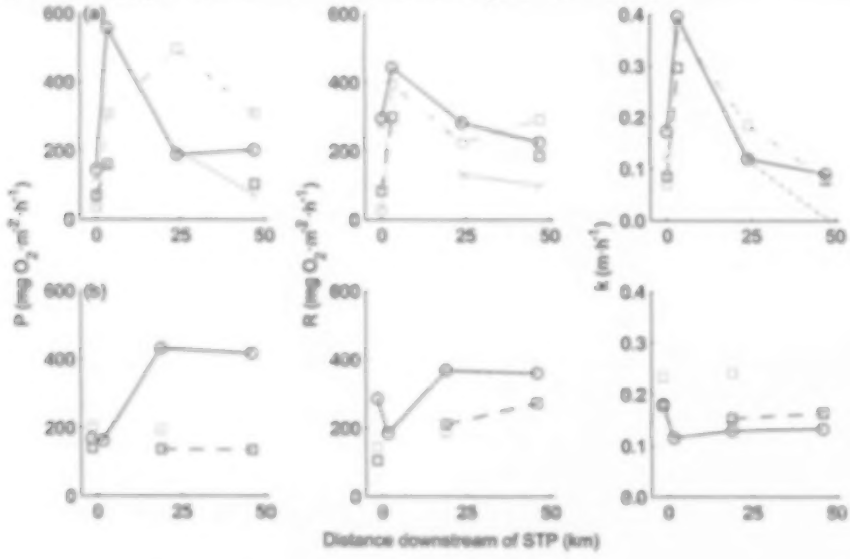
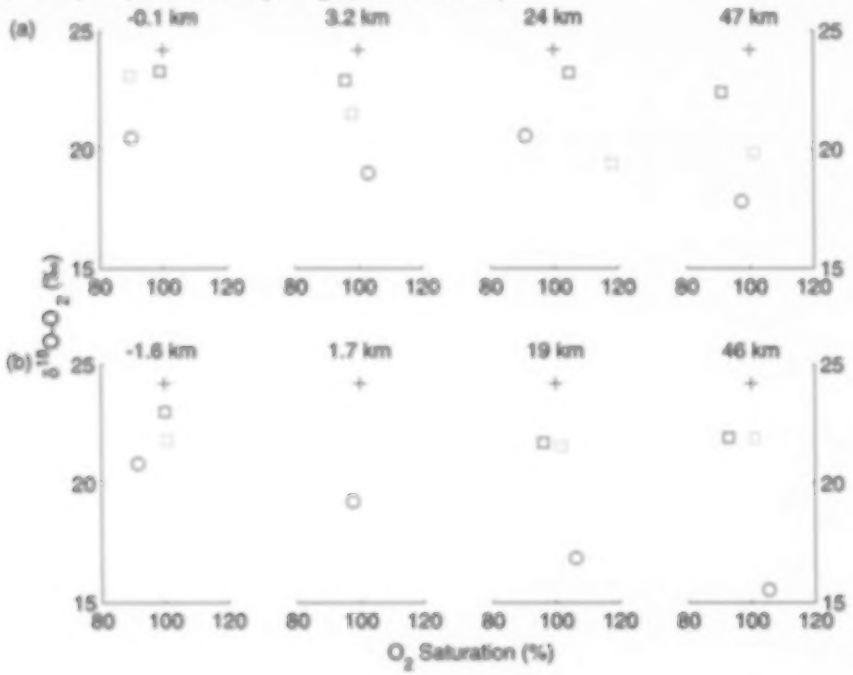


Table 2. Field variables and PoRGy model results for the seasonal and longitudinal transects on the South Saskatchewan River.

	Meewasin (–1.6 km)			DN-STP Saskatoon (1.7 km)	Clarkboro (19 km)			Hague (46 km)	
Variables	13 July 2004	13 Oct. 2004	26 May 2005	13 July 2004	15 July 2004	14 Oct. 2004	26 May 2005	15 July 2004	14 Oct. 2004
Known variables									
$\delta^{18}O$-H_2O (‰)	–16.1	–15.9	–16.2	–16.1	–15.6	–16.4	–17.0	–15.7	–15.1
Latitude (°N)	52.056	52.056	52.056	52.056	52.321	52.321	52.321	52.498	52.498
Longitude (°W)	106.422	106.422	106.422	106.422	106.458	106.458	106.458	106.258	106.258
Altitude (m above sea level)	470	470	470	470	462	462	462	454	454
Day of year	195	287	146	195	197	288	146	197	288
Year (CE)	2004	2004	2005	2004	2004	2004	2005	2004	2004
Input variables for model fit									
P_{max} (mg·m^{-2}·h^{-1})	651	1583	785	627	1672	1596	759	1615	1591
R_{20} (mg·m^{-2}·h^{-1})	238	181	221	155	305	367	287	295	485
k (m·h^{-1})	0.180	0.178	0.235	0.116	0.129	0.153	0.242	0.133	0.163
α_R	0.999	0.984	1.000	0.995	0.988	0.995	0.992	0.994	0.996
Calculations and model fit									
P:*R*:*G*	1.18:1.98:1	1.18:0.88:1	1.42:1.01:1	1.76:2.00:1	1.99:1.70:1	1.12:1.71:1	1.53:1.48:1	1.75:1.51:1	0.78:1.56:1
P:*R*	0.59:1	1.34:1	1.41:1	0.88:1	1.17:1	0.65:1	1.04:1	1.15:1	0.50:1
P (mg O_2·m^{-2}·h^{-1})	170	142	203	163	432	139	196	417	137
R (mg O_2·m^{-2}·h^{-1})	286	106	144	186	369	212	189	361	273
G^* (mg O_2·m^{-2}·h^{-1})	145	122	142	93	217	124	128	239	175
r^2 (saturation)	0.97	0.87	0.77	0.97	0.98	0.98	0.96	0.97	0.98
r^2 (isotopes)	0.32	0.09	0.04	0.84	0.90	0.56	0.06	0.94	0.60

Note: The kilometre value in parentheses after the transect name represents the distance above or below the Saskatoon STP. G^* is gross G, i.e., the sum of the influx and efflux, not their difference.

Fig. 11. Mean O_2 saturation and $\delta^{18}O$-O_2 value cross plots in (*a*) the Bow River and (*b*) the South Saskatchewan River as a function of distance downstream from the sewage treatment plant (STP) outfalls in July 2004 (circles), October 2004 (squares), and May 2005 (shaded squares). Air-saturated water (ASW) is shown as a plus sign (+) in each cross plot.



15.5‰, respectively. Using an α_R value of 0.986, the means would have been 107% and 16.4‰. Hence, the main effect of substantially altering α_R was to cause the model output to not visually fit half of the $\delta^{18}O$-O_2 data, in particular the data from the late afternoon and nighttime (top left in a cross plot of O_2 vs. $\delta^{18}O$-O_2). At those times, the model overestimated the $\delta^{18}O$-O_2 values (Venkiteswaran et al. 2008). This contrasted with findings suggesting that α_R values ranging from 0.972 to 1.000 had no effect on modelling output (Parker et al. 2005), but confirmed other findings of high oxygen isotopic model sensitivity to α_R (Quiñones-Rivera et al. 2009).

The comparative or differential effect of nitrification of STP-derived ammonia versus community respiration on dissolved O_2 and isotope fractionation in river systems remains unknown. We acknowledge that this could be an additional variable (Dunnette and Avedovech 1983) that we have encompassed within community R; however, we are unaware of any papers demonstrating O_2 isotope fractionation specifically due to nitrification.

General effects of STPs on whole-riverine metabolism

Our data from the Bow River and SSR suggested that combined O_2 and $\delta^{18}O$-O_2 diel curves constitute a powerful tool to quantify changes in integrated whole-community metabolism resulting from point-source STP effluents. The spatial and seasonal PoRGy modelling results indicated that the STPs had a quantifiable effect on the whole-community metabolism of these two rivers. Nutrient additions to rivers from STP effluents invariably increase aquatic metabolism (Wetzel 2001). STP outfalls, although they are treated to remove a large portion of carbonaceous biological O_2 demand (BOD), currently remain as major point sources of nitrogen and phosphorous to rivers (Chambers et al. 1997). Thus, the net effect of STPs on river metabolism can be viewed as a combination of cultural eutrophication from the stimulation of P and increased R from carbonaceous and nitrogenous BOD and elevated total phosphorous.

Taken altogether, our O_2 isotopic data and PoRGy modelling results from the Bow River and SSR revealed that primary productivity rates increased by 60%–90% in the spring and summer as a direct result of STP inputs to the rivers, and that productivity exhibited seasonal effects that were related mainly to light conditions and water temperature. Aquatic community R rates increased by 20%–90% as a direct result of STP inputs to the rivers and also appeared to be controlled mainly by the seasonal patterns of river water temperature (Figs. 5, 6, and 10). In general, P increased more than R at all sites downstream of the STPs, resulting in higher mean O_2 concentrations (Fig. 11) in addition to larger diel swings in O_2 concentration. Any increases in BOD and thus R from the STP effluents were completely masked by the higher increases in P rates at sites within 50 km of the STP. However, these increases in P over R cannot be sustained on an annual basis or with further distance downstream — eventually R must exceed P unless sufficient autochthonous material is buried without further decomposition. At the most distal sites in our study, transects 50 km downstream of the STPs, overall P:R and thus the mean O_2 concentrations began to decline. Likely, the

hinge point of the relative effect on *P* versus *R* will change with season and also perhaps water depth as affected by discharge. By fall, the effect on *R* exceeds that of *P* even though the mean $\delta^{18}O\text{-}O_2$ (Fig. 11) showed that *P* continued to be stimulated in both rivers above the rates observed at the control sites upstream of the STP. Hence, one implication is that the scale length of the effects of STP effluents on these rivers is likely much longer than 50 km and will be seasonally dependant. As O_2 solubility is lower at higher temperatures, and if flows are also lower in mid-summer (true for the SSR in our study but not the Bow River), then the summer becomes a critical period for river management in areas close to STP outfalls. However, under ice-covered conditions, the effects on *R* from summer increased *P* productivity (residual organic matter decay) may persist downstream far beyond 50 km as gas exchange is restricted by ice cover.

Hence, one hypothetical water quality implication of these differences in seasonal effects on *P* and *R* in terms of nutrient management would be (*i*) to export proportionally more phosphorous during the dark, cold months when *P* rates are low and do not increase downstream of the STPs and (*ii*) to export more organic carbon and nitrogen during the cold months when *R* rates are lowest. Exported labile organic carbon, whether from the STP effluent in the fall and winter or from elevated primary production rates during the spring and summer, is eventually transported and deposited in downstream pools and reservoirs where it is available to fuel O_2-consuming decomposition. Clearly, differential TP, nitrogen, and organic carbon STP discharge optimization strategies would be a costly and difficult undertaking from a municipal STP engineering perspective and unlikely to happen in most cases, but may need to be considered in the most vulnerable of situations.

Finally, the critical dependence of O_2 concentrations on water temperature and gas exchange and the concomitant interplay of *P*, *R*, and *G* confounds simplistic comparison of O_2 dynamics among rivers and sites. Here we have demonstrated that O_2 and $\delta^{18}O\text{-}O_2$ diel curves are a powerful tool to enable quantification of whole aquatic community metabolism changes arising from point-source STP impacts located at upstream and downstream sites. The $\delta^{18}O\text{-}O_2$ clearly showed and allowed us to quantify the effect of STPs on community metabolism at distances exceeding 50 km downstream of the source.

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Detecting and correcting underreported catches in fish stock assessment: trial of a new method

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Abstract: Landings from fisheries are often underreported, that is, the true landings are greater than those reported. Despite this bias, reported landings are widely used in fish stock assessments, and this might lead to overoptimistic exploitation strategies. We construct a statistical stock assessment model that accounts for underreported landings using the theory of censoring with sequential population analysis (SPA). The new model is developed and implemented specifically for the cod stock (*Gadus morhua*) from the southern Gulf of St. Lawrence (Canada). This stock is known to have unreported overfishing during 1985–1992. We show in simulations that for this stock, the new censored model can correctly detect the problematic landings. These corrections are nearly insensitive to subjective boundaries placed on real catches and robust to modifications imposed in the simulation of landings. However, when surveys are too noisy, the new SPA for censored catches can result in increased uncertainty in parameters used for management such as spawning stock biomass and age-structured stock size.

Résumé : Les relevés de pêche effectués lors des débarquements sous-estiment souvent la pêche réelle. Malgré ce biais, ces relevés sont largement employés pour l'évaluation des points de repère biologiques, ce qui peut mener à une exploitation trop optimiste des ressources. Nous construisons un modèle statistique pour l'estimation des stocks de poissons qui permet l'utilisation de relevés de pêches sous-estimés, en incorporant de la censure au modèle d'analyse de population séquentielle. Ce nouveau modèle est ensuite développé et mis en oeuvre pour le stock de morue (*Gadus morhua*) dans le sud du Golfe du Saint-Laurent (Canada) qui a subi une forte surexploitation non relevée pendant les années 1985–1992. Nous montrons à l'aide de simulations que le modèle avec censure détecte correctement les relevés de pêche problématiques. Les corrections sont peu sensibles à des bornes arbitraires imposées aux vraies prises et robustes à des modifications du modèle pour la simulation des relevés. Cependant, lorsque les enquêtes sont bruitées, le nouveau modèle avec prises censurées peut donner des résultats peu précis pour des paramètres utilisés pour la gestion, tels que le niveau du stock ou des mesures de stock par âge.

Introduction

The management of commercial fisheries and especially the determination of the total allowable catch (TAC) usually rely on information from population dynamics models. Cohort models are often used to assess stocks when an age structure can be established. Typically, observed data are total catches per year, catch proportions at age, and annual age-based abundance indices (Pope 1988) and other biological data on growth and maturation rates.

Common analytic assessment methods rely on the assumption that the catches are known without error. To be more precise, the catches are assumed to be measured without observation errors by harvesters and reported accurately to control authorities. This is the basis of the ADAPT method introduced by Gavaris (1988), which is commonly used when modelling Northwest Atlantic groundfish stocks and for extended survivor analysis (Shepherd 1999). Both of these approaches are versions of sequential population analysis (SPA; cf. Lassen and Medley 2000). However, in many cases, the reported landings are suspected to be lower than the true catches because of discards of less valuable fish, errors in reports, illegal fishing, control difficulties, etc. (Pitcher et al. 2002). For example, Punt et al. (2006) indicated that discard proportions in trawl fisheries could be as large as 50%. Note, however, that overreporting can also occur because of misidentifications (Walsh et al. 2007) or when fishermen want to secure track records or induce market distortion (Pearson 2001). Such errors will introduce bias in estimated population sizes derived from SPA. Mohn (1999), Cadigan and Farrell (2005), and Radomski et al. (2005), among others, have highlighted, through simulation and sensitivity studies, the limitations of ADAPT-type methods assuming that catches are measured without error.

Models with observation errors have been applied to catch-at-age data by Fournier and Archibald (1982), Gudmundsson (1986), and Aanes et al. (2007) and to total catch data by Kimura (1990), Patterson (1998), and Nielsen and Lewy (2001). Though the normal distribution has sometimes

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been used (Lewy 1988), the lognormal distribution has been the most frequent choice for the catch observation error and survey data error. The models with observation errors assume that the reported landings, while uncertain, are unbiased with respect to the real catches.

The quality of stock assessment is directly linked to the quality of catch data; therefore, correcting underreported catches is important (Pitcher et al. 2002). Numerous correction approaches have been considered. For instance, misreported catches have been estimated by comparison of landings with fishmeal factory outputs (Castillo and Mendo 1987; Patterson et al. 1990; Pitcher and Stokes 1990). Another approach is to place observers onboard the fishing vessels to evaluate the discards and correct the official landings (Knuckey et al. 1999). Among others, Fox and Starr (1996) and Walsh et al. (2002, 2007) have compared reports from logbooks and observers to correct catch histories. Knowing the particular problems associated with a specific fishery such as its history and economic stakes, Pitcher et al. (2002) proposed corrections for potentially misreported catches. Punt et al. (2006) included data on discards in Bayesian population assessments, building hypotheses on the discarding pattern of fishing fleets. These approaches require additional data or information that will usually not be available for many stock assessments or for the entire time frame on which the stock is based.

In this article, we develop a methodology, based only on typically available data, to estimate the magnitude of underreporting when catches are measured with error. It thus can help to make up for the lack of data needed for direct corrections (usually obtained from observers). The methodology relies on two steps: first, a statistical detection of underreported catches, and then a correction of the catch history. Our approach is motivated by Hammond and Trenkel (2005), who considered catches as censored observations. "Censoring" refers to a technique commonly used in survival analysis and industrial reliability (Lawless 2003), which, however, seems not to have been considered much in fish stock assessment. A censored observation is one for which we do not know the exact value but about which we have partial information such as a lower bound (right censoring) or an interval known to cover the exact value (interval censoring).

Hammond and Trenkel (2005) proposed a censoring framework to model total landings (L_y^*) that are lower bounds for the total catches (C_y^*) that should have been observed with error and to constrain corrections ($C_y^* - L_y^*$) to reasonably low values. They assumed that the unknown value of C_y^* was in the interval $[L_y^*, 2L_y^*]$. These constraints were included in a Schaefer surplus production model, and parameters were estimated using Bayesian methods. They concluded that their censored model improved estimates of maximum sustainable yields and depletion indices, and that handling misreporting with censored catches can outperform some traditional assessment methods.

This paper extends the censoring framework to age-structured models with a particular focus on catch estimation and detection of misreporting. The model is developed specifically for the southern Gulf of St. Lawrence (SGSL; 4T in Fig. 1) cod stock. The assessment information is provided by Chouinard et al. (2006), and commercial catches are known to be underreported in some years. We consider censored total catches (i.e., summed over ages) because the age-composition estimates are thought to be sufficiently accurate for this stock. For example, cohorts can be clearly tracked over time. Pope (1988), Patterson (1998), and Cotter et al. (2004) also favored adding observation error to the total catch only because it is often reported independently of the landings age structure, which can be estimated more reliably.

The paper is organized as follows. First, we present the features of the models used for the assessment of the SGSL cod stock and provide the likelihood terms associated with censored catches. Focusing on underreporting, we assume that a censored observation C_y^* lays in an interval $[L_y^*, \beta_y L_y^*]$. It is assumed that stock experts can propose a reasonable value for β_y in most cases, but a less restrictive framework with $\beta_y = \infty$ is also considered. We use maximum likelihood estimation of the model parameters, with a simulated annealing algorithm to numerically maximize the likelihood and get standard errors. The effectiveness of incorporating censoring is highlighted in simulations using several censoring strategies. A heuristic method for the detection of underreporting is presented. The impact of catch corrections on SPA estimates of stock size is also discussed. Finally, extensions of the methodology to other stocks are considered in the Discussion.

Materials and methods

We consider the evolution of an exploited marine population, such as the SGSL cod stock, through years $y = 1, \ldots, Y$ and A age classes indexed by $a = 1, \ldots, A$. Without loss of generality, A can be an $A+$ class, aggregating the population for ages $\geq A$.

Three notations are used to differentiate the true catches, the observed catches, and the landings. First, denote the true total catches by $\mathbf{C} = (C_1, \ldots, C_Y)$, which are the exact numbers of fish taken out of the water. Next, denote the measured catches as $\mathbf{C}^* = (C_1^*, \ldots, C_Y^*)$, which are, in mean, equal to the true catches $\mathbf{C}$ but incorporate some observational errors. Finally, denote $\mathbf{L}^* = (L_1^*, \ldots, L_Y^*)$ as the total landings reported by the harvesters.

The framework

Observed catches are assumed to be linked to the real catches C_y through the typical observation equation

$$(1) \qquad C_y^* = C_y \exp(v_y), \quad y = 1, \ldots, Y$$

where $v_y \overset{\text{iid}}{\sim} \mathcal{N}(-\sigma^2/2, \sigma^2)$. Note that the mean $-\sigma^2/2$ is required so that $E[C_y^*] = C_y$. Let $\theta_1 = (C_1, \ldots, C_Y, \sigma^2)$ denote the set of $Y + 1$ parameters of primary interest. If the C_y^* are known, then the log-likelihood for θ_1 associated with eq. 1 is

$$(2) \qquad \ell_C(\theta_1; \mathbf{C}^*) = -Y \log \sigma - \frac{1}{2\sigma^2} \sum_{y=1}^{Y} \left(\log C_y^* - \log C_y + \frac{1}{2}\sigma^2 \right)^2$$

Because there are only Y independent observations, more data are required for a nontrivial and statistically valid assessment of θ_1, or the dimension of θ_1 must be reduced. Because it seems quite difficult and arbitrary to connect C_y to C_{y-1} through a deterministic relationship with a small number of parameters, finding additional data is more desirable. We use survey indices to define a second term in the log-likelihood.

We assume that annual age-based survey indices $\{I^*_{a,y}\}$ of stock size are related to stock abundance $N_{a,y}$ through the observation equation

$$(3) \quad I^*_{a,y} = Q_a N_{a,y} \exp(\varepsilon_{a,y}), \quad y = 1, \ldots, Y,\ a = 1, \ldots, A$$

where $Q_1, \ldots, Q_A$ are catchability coefficients and $\varepsilon_{a,y} \overset{\text{iid}}{\sim} \mathcal{N}(0, \tau^2)$. From eq. 3, $E(I^*_{a,y}) = Q_a N_{a,y} \exp(\tau^2/2)$. We do not require $E(\varepsilon) = 1$ because the bias term $\exp(\tau^2/2)$ only affects the value of Q_a and not the estimation of the $N_{a,y}$ (Aanes et al. 2007). Let $\mathbf{I}^*$ denote the matrix of survey indices. The associated log-likelihood, ignoring the bias term, is

$$(4) \quad \ell_I(\theta; \mathbf{I}^*) = -AY \log \tau - \frac{1}{2\tau^2} \sum_{A,Y} (\log I^*_{a,y} - \log Q_a - \log N_{a,y})^2$$

where θ denotes the vector of all the parameters, including τ^2, the catchabilities, and all $N_{a,y}$. When the $N_{a,y}$ are modeled as functions of C_y and of some baseline abundances, the survey indices supplement the information in eq. 2 to estimate the C_y.

We assume that the abundance $N_{a,y}$ follows an exponential decline at a rate $Z_{a,y} = F_{a,y} + M_{a,y}$, where $F_{a,y}$ is the fishing mortality rate and $M_{a,y}$ is the natural mortality rate:

$$(5) \quad N_{a+1,y+1} = N_{a,y} \exp(-Z_{a,y})$$

We make the common assumption that $M_{a,y}$ is known for all ages and years. We consider uncertainty about $M_{a,y}$ in the Discussion. The real catch-at-age $C_{a,y}$ is related to $N_{a,y}$ and $F_{a,y}$ through the Baranov equation:

$$(6) \quad C_{a,y} = N_{a,y} \frac{F_{a,y}}{Z_{a,y}} \{1 - \exp(-Z_{a,y})\}, \quad a = 1, \ldots, A-1,\ y = 1, \ldots, Y$$

An F constraint (Gavaris and Ianelli 2002) is used to reduce the number of parameters:

$$(7) \quad F_{A,y} = \frac{1}{2}(F_{A-1,y} + F_{A-2,y}), \quad y = 1, \ldots, Y$$

The rationale behind this choice is the similarities in size between the fish of the oldest ages, which should imply similar fishing mortality. Pope's approximation (Pope 1972) of eq. 6 leads to

$$(8) \quad N_{A,y} = \frac{C_{A,y} \exp(-M_{A,y}/2)}{1 - \exp(-F_{A,y})}, \quad y = 1, \ldots, Y$$

Hence, using eqs. 5, 6, and 8, all pairs $(N_{a,y}, F_{a,y})$ can be computed knowing the catches at age and the survivors in the last year, $N_{a,Y}$, $a = 1, \ldots, A-1$.

Finally, the $C_{a,y}$ are obtained as the product of C_y and the catch proportions at age, $\rho_{a,y}$. As in Patterson (1998), we assume that the $\rho_{a,y}$ are estimated with negligible errors by survey and biological sampling, independently from the landings L^*_y. This hypothesis is reasonable for stocks with industrial fisheries such as the SGSL cod stock that have good port sampling of landed fish, which results in accurate estimation of the age composition of the catch. In the Discussion, we consider how this assumption can be relaxed. Hence, we reduce the parameter vector to $\theta = (\theta_1, \theta_2)$, where

$$(9) \quad \theta_1 = (C_1, \ldots, C_Y, \sigma^2)$$

and

$$(10) \quad \theta_2 = (N_{1,Y}, \ldots, N_{A-1,Y}, Q_1, \ldots, Q_A, \tau^2)$$

Correctly reported catches

Two notions of "correct" reporting can be considered, leading to two population models.

ADAPT model

Our first population model assumes that there is no measurement error, namely $C_y = C^*_y = L^*_y$. Thus $\sigma = 0$, θ is reduced to θ_2, and the assessment of biological quantities is made by maximizing $\ell_I(\theta; \mathbf{I}^*)$ only. Because the likelihood is derived from the lognormal, its maximization is similar to the least squares estimation promoted by Gavaris (1988) and Rivard and Gavaris (2003) under the name "ADAPT". Despite the increasing number of research articles that take into account catch measurement error, ADAPT remains one of the most widely used stock-assessment models (Lassen and Medley 2000; Patterson et al. 2001).

FA model

In the FA model, from Fournier and Archibald (1982), it is assumed that observed catches C^*_y are noisy but unbiased measures of the C_y and that there is no misreporting, i.e., $L^*_y = C^*_y$. The model is also defined by the parameter θ and the main term of the log-likelihood $\ell(\theta) = \ell_C(\theta_1; \mathbf{C}^* = \mathbf{L}^*) + \ell_I(\theta; \mathbf{I}^*)$.

Misreported catches

In the censored FA model, some L^*_y are lower bounds for C^*_y. Each reported landing L^*_y is associated with a doublet $(\alpha_y, \beta_y) \in I\!R_+ \times [\alpha_y, \infty)$ such that $\alpha_y L^*_y \le C^*_y \le \beta_y L^*_y$, where C^*_y is an unknown realization of the observed catches described in eq. 1. The variable C^*_y is said to be interval censored. If the catch is not misreported, then $\alpha_y = \beta_y = 1$. We focus here on underreporting and use $\alpha_y = 1$ and $\beta_y \ge 1$ throughout the paper.

In survival analysis, the contribution of an interval censored observation $(\alpha_y L^*_y, \beta_y L^*_y)$ to the likelihood is usually expressed as the probability that C^*_y belongs to $(\alpha_y L^*_y, \beta_y L^*_y)$, i.e., $F_{C^*_y}(\beta_y L^*_y) - F_{C^*_y}(\alpha_y L^*_y)$, where $F_{C^*_y}$ is the lognormal cumulative distribution function (cdf) of C^*_y emanating from eq. 1; see chapter 2 of Lawless (2003). To show that this is appropriate for underreported catches, assume that $C^*_y = u_y L^*_y$, where u_y follows the uniform distribution on $[\alpha_y, \beta_y]$. In other words, once α_y and β_y are specified, all values in the interval $(\alpha_y L^*_y, \beta_y L^*_y)$ are equally likely to be the

true value of C_y^*. The likelihood term for a censored C_y^* is then

$$\frac{1}{\beta_y - \alpha_y}\int_{\alpha_y}^{\beta_y} f_{C_y^*}(u_y L_y^* | \alpha_y, \beta_y, L_y^*, u_y)\, du_y$$

where $f_{C_y^*}$ is the density of $F_{C_y^*}$. This is proportional to $F_{C_y^*}(\beta_y L_y^*) - F_{C_y^*}(\alpha_y L_y^*)$, the standard likelihood contribution for interval-censored variables presented above. Thus, the likelihood for censored catches can be constructed as a standard likelihood for interval-censored lifetime data. If $\beta_y = \infty$, then C_y^* is right-censored, as only a lower bound for its unknown value, $\alpha_y L_y^*$, is available. Its likelihood contribution then reduces to the survival function $1 - F_{C_y^*}(\alpha_y L_y^*)$.

Finally, denote $\mathbf{Y}_{[U]}$ the subset of $\{1, \ldots, Y\}$ such that the $(C_y^*)_{y \in \mathbf{Y}_{[U]}}$ are reported correctly, $\mathbf{Y}_{[U]} = \{k \in \{1, \ldots, Y\}: \alpha_k = \beta_k = 1\}$, and denote Y_U the cardinal of $\mathbf{Y}_{[U]}$. Similarly, denote $\mathbf{Y}_{[C]} = \{1, \ldots, Y\}/\mathbf{Y}_{[U]}$ the subset of years with misreported catches, and let $Y_C = Y - Y_U$ denote the number of censored catches. Then the log-likelihood of observed catches $\ell_C(\theta_1; \mathbf{C}^*)$, given in eq. 1, is replaced by

$$(11)\quad \ell_C(\theta; \mathbf{L}^* | \alpha_y, \beta_y) = \sum_{y \in \mathbf{Y}_{[C]}} \log\left\{\Phi\left(\frac{\log \beta_y L_y^* - \log C_y + \frac{1}{2}\sigma^2}{\sigma}\right) - \Phi\left(\frac{\log \alpha_y L_y^* - \log C_y + \frac{1}{2}\sigma^2}{\sigma}\right)\right\} - Y_U \log \sigma - \frac{1}{2\sigma^2}\sum_{y \in \mathbf{Y}_{[U]}}\left(\log L_y^* - \log C_y + \frac{1}{2}\sigma^2\right)^2$$

with $\Phi(\cdot)$ being the cdf of the standard normal distribution.

Maximum likelihood estimation

Profile likelihoods

Consider the parameter vector θ whose component subvectors (θ_1, θ_2) are detailed in eqs. 9–10. We focus on obtaining the maximum likelihood estimator (MLE) of catches

$$\hat{\theta}_1 = \arg\max_{\theta_1} \ell\left(\theta_1, \hat{\theta}_2(\theta_1)\right)$$

where $\hat{\theta}_2(\theta_1)$ is the profiled MLE obtained by maximizing eq. 4 for given θ_1. In other words, $\hat{\theta}_2(\theta_1)$ is the ADAPT estimate of stock size obtained with the landings set equal to the catches $C = (C_1, \ldots, C_Y)$ in θ_1.

Denote by $\mathbf{S} = (N_{1,Y}, \ldots, N_{A-1,Y})$ the set of survivors. Recall that all the $N_{a,y}$ are functions of $(\mathbf{C}, \mathbf{S})$. Catchabilities and variances can be replaced in eq. 4 by their conditional MLE, leading to a profile loglikelihood $\ell_I^p(\mathbf{C}, \mathbf{S}; \mathbf{I}^*)$ based on the observed survey indices. The MLE of τ is indeed

$$(12)\quad \hat{\tau}^2(\mathbf{C}, \mathbf{S}) = \frac{1}{AY}\sum_{a=1}^{A}\sum_{y=1}^{Y}\left(\log I_{a,y}^* - \log \hat{Q}_a(\mathbf{C}, \mathbf{S}) - \log N_{a,y}(\mathbf{C}, \mathbf{S})\right)^2$$

As suggested by Patterson (1998), we add an estimation constraint on the series of catchabilities at age $(Q_1, \ldots, Q_A)$. To be biologically plausible, real catchability should be a smooth function of age, say $Q(a|\delta)$, depending on a parameter vector δ. Following Patterson (1998), we choose $Q(\cdot|\delta)$ as a natural cubic spline function. The rationale for this choice and additional details about the estimation of δ are given in Appendix A. Replacing such a nuisance parameter vector by ad hoc estimators in the likelihood is considered by Gong and Samaniego (1981). They called the resulting estimates pseudo maximum likelihood. They show that under suitable regularity conditions, pseudo and true maximum likelihood estimates have similar sampling properties. Thus we overlook this slight deviation from maximum likelihood estimation and consider

$$\ell_I^p(\mathbf{C}, \mathbf{S}; \mathbf{I}^*) = -AY \log \hat{\tau}^2(\mathbf{C}, \mathbf{S}) + \text{constant}$$

as the profile log-likelihood for the estimation for $(\mathbf{C}, \mathbf{S})$.

In a similar way, σ^2 can be profiled out of the catch log-likelihoods eqs. 2 and 11. In the uncensored framework $(C_y^* = L_y^*)$, a closed form expression for $\hat{\sigma}^2(\mathbf{C})$ maximizing eq. 11 is given by

$$(13)\quad \hat{\sigma}^2(\mathbf{C}) = 2\left\{\sqrt{1 + \frac{1}{Y}\sum_{y=1}^{Y}(\log L_y^* - \log C_y)^2} - 1\right\}$$

In a censored framework, a simple Newton–Raphson method starting from eq. 13 can be used to compute $\hat{\sigma}^2(\mathbf{C})$. The profile catch log-likelihood is then

$$\ell_C^p(\mathbf{C}; \mathbf{L}^*) = \ell_C(\mathbf{C}, \hat{\sigma}^2(\mathbf{C}); \mathbf{L}^*)$$

Estimation of the FA parameters and their uncertainties

Our objective is to maximize the following profile log-likelihood:

$$(14)\quad \ell^p(\mathbf{C}, \mathbf{S}) = \ell_C^p(\mathbf{C}; \mathbf{L}^*) + \ell_I^p(\mathbf{C}, \mathbf{S}; \mathbf{I}^*)$$

Nelder–Mead simplex methods (Lange 2001) have been successfully used to fit ADAPT-type models, namely to estimate $\hat{\mathbf{S}}(\mathbf{C})$ for a given vector $\mathbf{C}$. Starting points for the survivors may simply be chosen as multiples of the landings at age reported in year Y. In FA models, however, our experience has shown that a two-step procedure that first maximizes eq. 14 with respect to $\mathbf{S}$ for fixed $\mathbf{C}$ with the ADAPT algorithm and then maximizes $\ell^p(\mathbf{C}, \hat{\mathbf{S}}(\mathbf{C}))$ with respect to $\mathbf{C}$ is numerically prohibitive. For this reason, total catches and survivors have been estimated simultaneously. Thus we redefine θ as $(\mathbf{C}, \mathbf{S})$ to simplify the notation, as the variance components σ^2 and τ^2 have been profiled out of eq. 14.

From a theoretical viewpoint, classic frequentist tools such as Hessian inversion (Patterson et al. 2001) for the estimation of parameter uncertainty are not relevant for a FA model. Indeed, the justification of Hessian inversion is based on the asymptotic normality of $\hat{\theta}$; see Koenker and Machado (1999) for additional details. In the FA model, the dimension of θ increases linearly with the size Y of the data, which invalidates the direct application of classical asymptotic results to this model. Bootstrap methods have also been considered. However, these methods also require an asymptotic justification and were found to be computationally prohibitive for the SPA models that we consider.

We therefore adopted the following scheme. (*i*) Estimate $\widehat{\theta}$ using a Nelder–Mead simplex method. (*ii*) Attempt to improve $\widehat{\theta}$ with a sampling method that avoids local maxima and provides Monte Carlo estimates of uncertainty for calculating confidence intervals. We used simulated annealing (SA) for this purpose. Theoretical justifications can be found in Van Laarhoven and Arts (1987), and a didactic presentation with an overview of the main results is provided in Robert and Casella (2004, § 5.2.3). This sampling method is often used to find the mode of a posterior distribution in a Bayesian framework, for instance by Andrieu and Doucet (2000) and Doucet et al. (2002). Because the MLE is the posterior mode when all priors are uniform, the SA algorithm can be used to estimate θ and build confidence regions; this is described in Appendix A.

Illustration

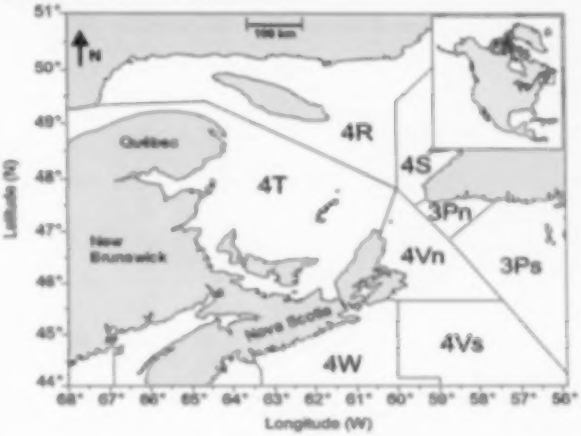
We fit the models to data from Chouinard et al. (2006) on the cod stock in the southern Gulf of St. Lawrence (SGSL, Canada, NAFO Subdivisions 4T and 4Vn; cf. Fig. 1) between 1971 and 2005 ($Y = 35$ years). This stock is recognized as having severely suffered from overfishing (Swain and Chouinard 2008). A simulation study is also carried out to investigate whether various censored FA models can identify underreporting periods and provide good estimates of real catches.

An assessment of SGSL cod catches

The SGSL cod stock has remained depleted since a fishing moratorium was imposed in 1993. The fishery was closed between September 1993 to May 1998. It was reopened with a TAC of 3000 tonnes (t) for an index fishery in 1998. The TACs were set at 6000 t from 1999 to 2002. The directed fishery was closed again in 2003 but was reopened with a TAC of 3000 t in 2004. In 2005, the TAC was increased to 4000 t. When the directed fishery was closed, removals were only due to scientific fishery. The collapse of this stock and others in the Northwest Atlantic in the early 1990s has been attributed to overfishing (Sinclair and Murawski 1997), in the sense that the TACs were exceeded and underreporting occurred. High overfishing for SGSL cod has been suspected during the years 1985–1992, just before the alarming decline of the resource. In addition, note that the cod population has suffered from an important increase of the natural mortality in the mid-1980s (Chouinard et al. 2006). In the model, the known rates of mortality are $M_{a,y} = 0.2$ from 1971 to 1985 and $M_{a,y} = 0.4$ from 1986 to 2005 for all ages, as suggested by Chouinard et al. (2006). We used the data reported in their paper for ages 2 to 15+. Thus $A = 14$ age classes were used in the model. The known catch proportions $p_{a,y}$ were calculated using the catch-at-age data of Chouinard et al. (2006).

We first fitted the ADAPT model with $L_y^\circ = C_y^\circ = C_y$ and the uncensored FA model with $L_y^\circ = C_y^\circ$, $y = 1, \ldots, Y$. The estimated catch history $\{C_y\}$ for the FA model is displayed (Fig. 2); for all practical purposes, it is equal to the reported landings $\mathbf{L}^\circ$, with a negligible standard deviation, $\widehat{\sigma} = 0.0043$. Because $\widehat{\tau}_{\text{FA}} \simeq \widehat{\tau}_{\text{ADAPT}} \simeq 0.68$, the fits of the uncensored FA model and of the ADAPT model are very similar. This high survey CV leads to a relatively imprecise

Fig. 1. Northwest Atlantic Fisheries Organization (NAFO) areas in the Gulf of St. Lawrence. Inset shows the study location off the eastern coast of Canada.



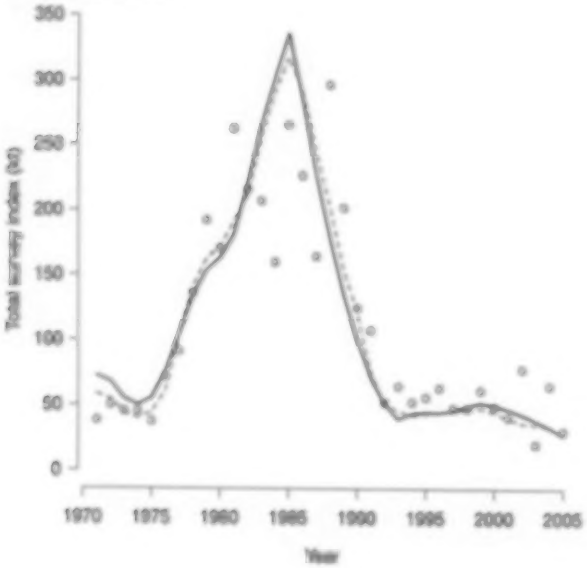
fit of the ADAPT-predicted indexes during the years 1980–1990 for which the observed indices are highly variable (Fig. 3). However, the magnitude of estimates in this period reflects an ADAPT overestimation of fish later caught between 1985 and 1989, resulting from catch underreporting. A continuous underreporting during the predecline period (1989–1991), associated with a pessimistic abundance underestimation, could explain the persistence of this underestimation after the decline.

Next we implemented the censored FA model with three censoring schemes, where a "censoring scheme" refers to the choice of censored years and corresponding β_y. We assumed $\alpha_y = 1$ for all years. Scheme 1 (broken lines in Fig. 2) included three time periods of censoring: 1985–1992, 1993–1998, and 2003 for which β_y is set to 2, 1.25, and 1.25, respectively. Scheme 2 (dotted lines in Fig. 2) assumed censoring only for the years 1971–1992 with $\beta_y = 2$. Scheme 3 (dashed–dotted lines in Fig. 2) assumed censoring for all years with $\beta_y = 2$.

Three time periods are always distinguishable in the estimated catch histories. The censored estimated catches C_y fit the landings L_y° for the years 1971–1984 (period P_1) and 1993–2005 (period P_3). However, during the period 1985–1992 (period P_2), we estimate $C_y \geq L_y^\circ$, and this difference appears more significant for the period 1988–1992. This is especially true under scheme 3. Furthermore, the estimates of σ and τ are similar for all schemes ($\widehat{\sigma} \simeq 0.072$ and $\widehat{\tau} \simeq 0.58$). The similarity of these results suggests that a crude censoring strategy has the ability to detect the years with underreported catches. The decrease of $\widehat{\tau}$ from 0.68 for the FA model to 0.58 for the censored FA model shows that adding censoring to the observation model for catches decreases the residual variance of the model for the indices by 27% ($= 1 - 0.58^2/0.68^2$). Thus censored catches give the assumed SPA model an additional flexibility that permits the indices data $I_{a,y}^\circ$ to be fitted more closely. As will be shown in the simulations below, this makes the censored FA model heavily reliant on the accuracy of the survey indices.

Fig. 2. Reported landings and total catch estimates according to the uncensored and three censored FA models.

Fig. 3. Observed and predicted total survey indexes for the southern Gulf of St. Lawrence cod: ADAPT, continuous line; censored FA model, broken line.

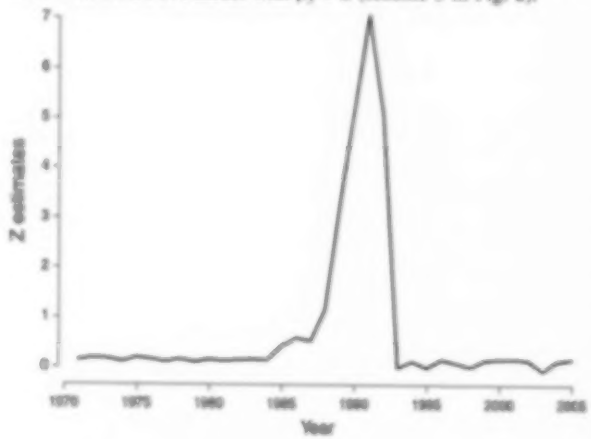


A heuristic detection of the underreported catches can been obtained with a time plot of

$$(15) \qquad Z_y = \frac{\log \widehat{C}_y - \log L_y^* + \frac{\widehat{\sigma}^2}{2}}{\widehat{\sigma}}$$

where $\widehat{C}_y$ and $\widehat{\sigma}$ are the MLEs of C_y and σ, respectively. Under the hypothesis that the L_y^* are not misreported, Z_y should approximatively follow a distribution with mean zero and unit variance. If the L_y^* are underreported during a certain period, the Z_y for this period should be significantly higher than during periods of correct reporting. The values of Z_y for the full-censored scheme 3 have been plotted (Fig. 4). The

Fig. 4. Evolution of values of Z_y estimated in the real case study by the full-censored FA model with $\beta_y = 2$ (scheme 3 in Fig. 2).



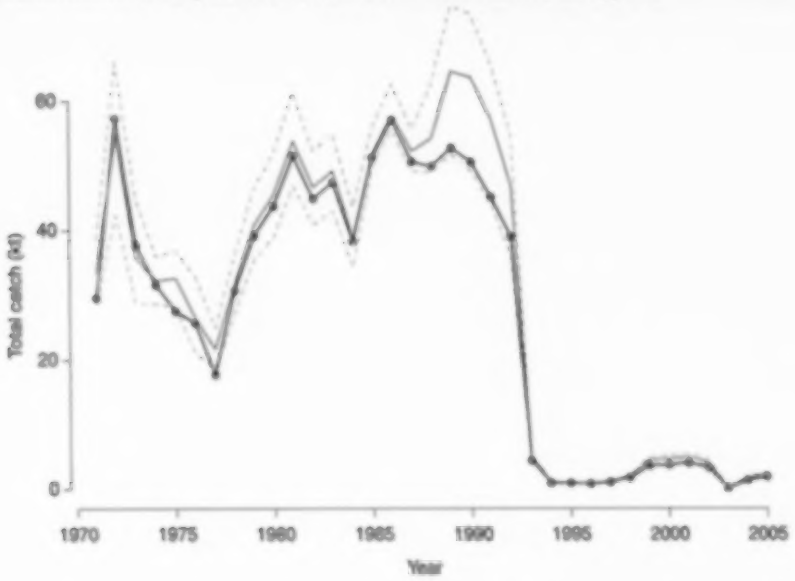
break point in the estimated catch history between years 1985 and 1992 appears quite clearly, in accordance with what was suspected to be the main period of underreporting.

For a reduced censoring scheme for 1985–1992 (period P_2) and assuming $\beta_y = 2$, the MLE of the total catches and an 80% confidence interval (estimated using the SA algorithm) are displayed (Fig. 5). Our motivation for using 80% was to show that the probability that true catches are equal or less than reported is only 10% during the period P_2.

Simulation study

The SGSL cod example suggests that incorporating censoring can lead to quantitative results that are in agreement with the experts' qualitative opinion about the real catches. We conducted a simulation study to investigate the accuracy of the catch estimators and of the biological indices used in fishing management. The Monte Carlo (MC) results are based on 80 data sets $\mathbf{X}^* = (\mathbf{I}^*, \mathbf{L}^*)$ independently simulated from the FA model with real catches, abundances, and

Fig. 5. Reported landings (line with circles) and MLE (shaded line) of total catches for the FA censored model (with confidence limits (broken lines)). Observed total catches for the years 1985–1992 are considered censored with $\beta_y = 2$.



catchabilities as estimated under the reduced censoring scheme at the end of the previous section (summarized in Fig. 5 and Appendix A, Table A1). Though 80 MC simulations may appear small, estimates of relative bias and root mean squared error (RMSE) stabilized after as few as 40 or 50 simulations. Four values (0.05 0.2, 0.4, 0.8) for the coefficient of variation (CV) of survey indices, defined here by $\sqrt{\exp(\tau^2) - 1}$, and two values (0.072, 0.2) for the CV of total catches ($\sqrt{\exp(\sigma^2) - 1}$) were used. The 0.05 value is realistic; a similar CV was observed by Chassot et al. (2009) for the cod stock in the northern Gulf of St. Lawrence (NGSL). Two schemes of censoring were used to simulate the observed landings. Denote by C_y^* a realization of the lognormal distribution (eq. 1).

In scheme A, the simulation model follows the assumptions made in the Material and methods section: a landing L_y^* for $y = 1985, \ldots, 1992$ is sampled from an inverse uniform distribution, i.e., $L_y^* = C_y^*/U_y$, where $U_y \sim \mathcal{U}[1, 2]$. In scheme B, the simulation model is different from the model in the Material and methods section and rather uses landings L_y^* for $y = 1985, \ldots, 1992$ given by $L_y^* = C_y^*/(1 + \kappa)$, for a fixed $\kappa \in [0, 1]$. Three values of κ (0.25, 0.5, and 0.75) are considered.

Comparing the model performance

Besides catches, the models are compared in terms of characteristics useful to fishery managers such as spawning stock biomass (SSB), recruitment (R), and fishing mortality rates (F). The SSB for year y (SSB_y) is defined as $\sum_{a=1}^{4} \omega_{a,y} p_{a,y} N_{a,y}$, where ω_a and $p_{a,y}$ are the mean weights and proportions mature at age a in year y, respectively, taken from tables 9 and 23 of Chouinard et al. (2006). The recruitment in year y is defined as the average size of the populations of biological ages 3 and 4, whereas the fishing rate in year y is taken as the average over all ages.

Relative biases and RMSEs are reported for these four sets of parameters. For instance, denote $\mathbf{C}_{o,\mathbf{p}} = (C_{o,1}, \ldots, C_{o,p})$ a p vector of true catches for p of the Y years under study. Denote $\widehat{\mathbf{C}}_{\mathbf{p}}^{(i)} = (\widehat{C}_1^{(i)}, \ldots, \widehat{C}_p^{(i)})$ the MLE of these catches for the ith simulated data set. The performance of the estimator of $\mathbf{C}_{o,\mathbf{p}}$ is measured using the (empirical) relative RMSE:

$$\text{(16)} \qquad \text{RMSE}(\mathbf{C}_{\mathbf{p}}) = \frac{\sqrt{\sum_{j=1}^{p} M^{-1} \sum_{i=1}^{M} \left(\widehat{C}_j^{(i)} - C_{o,j}\right)^2}}{\sqrt{\sum_{j=1}^{p} C_{o,j}^2}}$$

and the mean relative bias

$$\text{(17)} \qquad B(\mathbf{C}_{\mathbf{p}}) = \frac{1}{pM} \sum_{j=1}^{p} \sum_{i=1}^{M} \frac{\left(\widehat{C}_j^{(i)} - C_{o,j}\right)}{C_{o,j}}$$

where $M = 80$ is the number of simulated data sets. Thus when $B(\mathbf{C}_{\mathbf{p}}) > 0$ [respectively, $B(\mathbf{C}_{\mathbf{p}}) < 0$], the catches are overestimated [respectively, underestimated].

In the next section, the relative biases and RMSEs are aggregated for three periods: $P_1 = 1971$–1984, $P_2 = 1985$–1992, and $P_3 = 1993$–2005. Four models are fitted: ADAPT, CS_1 (the uncensored FA model), CS_2 (the censored FA model with known years of censoring), and CS_3 (the censored FA model that assumes censoring every year).

Simulation results

RMSE and relative biases obtained under scheme A are reported for four sets of parameters (Tables 1 and 2), as

Table 1. RMSE of total catches (C), annual fishing rates (F), spawning stock biomass (SSB), and recruitment (R), based on 80 simulated data sets for each combination of survey and catch CVs.

								CS_2						CS_3					
CV		ADAPT			CS_1			$\beta_2 = 2$			$\beta_2 = \infty$			$\beta_3 = 2$			$\beta_3 = \infty$		
Survey	Catches	P_1	P_2	P_3	P_1	P_2	P_3	P_1	P_2	P_3	P_1	P_2	P_3	P_1	P_2	P_3	P_1	P_2	P_3
C																			
0.8	0.2	**21**	**37**	**20**	100	98	99	94	80	99	115	91	131	230	113	427	246	124	430
0.8	0.072	**13**	**34**	**8**	99	98	97	78	73	97	95	82	101	155	114	185	155	135	194
0.4	0.2	**21**	**37**	**20**	101	100	100	93	70	101	93	78	102	169	75	346	172	76	370
0.4	0.072	**12**	**34**	**8**	99	99	97	77	65	96	79	67	96	122	67	152	123	71	177
0.2	0.2	**21**	**37**	**21**	100	99	101	92	48	101	92	48	102	137	62	274	172	76	370
0.2	0.072	**12**	**34**	**7**	99	100	101	82	53	99	83	57	103	106	62	132	110	63	163
F																			
0.4	0.2	**14**	**23**	**16**	99	98	99	89	93	101	101	100	105	136	105	134	139	120	143
0.4	0.072	**11**	**16**	**12**	100	102	101	86	83	99	94	92	99	131	101	136	137	117	137
0.2	0.2	**12**	**23**	**15**	97	96	99	91	63	96	97	69	101	101	65	102	108	72	108
0.2	0.072	**10**	**21**	**13**	100	104	100	90	60	98	92	64	99	95	61	108	99	71	107
0.05	0.2	**10**	**22**	**14**	96	100	97	82	57	91	82	61	92	81	59	101	85	62	103
0.05	0.072	**9**	**21**	**13**	95	105	96	78	55	91	79	56	91	82	57	100	83	59	104
SSB																			
0.4	0.2	**14**	**22**	**11**	103	101	115	158	165	123	160	171	132	232	227	247	240	221	248
0.4	0.072	**11**	**14**	**7**	102	98	105	150	140	115	153	139	121	225	209	226	231	213	245
0.2	0.2	**11**	**17**	**7**	100	98	111	131	92	104	138	99	110	224	163	324	235	168	332
0.2	0.072	**10**	**15**	**5**	102	99	109	127	84	98	132	86	102	211	156	328	221	160	334
0.05	0.2	**8**	**17**	**3**	100	99	105	99	62	96	102	64	95	155	81	232	153	83	232
0.05	0.072	**8**	**15**	**3**	101	99	103	101	57	91	99	58	94	149	73	221	151	72	224
R																			
0.4	0.2	**14**	**19**	**12**	99	102	128	158	124	141	159	127	150	227	187	218	234	187	224
0.4	0.072	**13**	**15**	**10**	99	100	131	151	112	130	155	122	143	230	183	202	228	185	211
0.2	0.2	**13**	**17**	**6**	99	98	109	118	83	122	111	89	116	189	131	240	195	136	254
0.2	0.072	**12**	**17**	**6**	100	99	115	102	68	98	106	72	101	181	125	227	187	133	235
0.05	0.2	**10**	**17**	**5**	96	97	107	101	59	114	103	64	115	157	88	189	162	85	194
0.05	0.072	**10**	**17**	**4**	98	99	105	92	51	109	93	54	104	144	68	177	141	71	181

Note: RMSEs are reported separately for the periods P_1 = 1971–1984, P_2 = 1985–1992, and P_3 = 1993–2005. ADAPT RMSEs are in bold type. Relative RMSEs with respect to ADAPT RMSEs, in percentage, are given in Roman type. Results are presented for the uncensored ADAPT and CS_1 models, for models with a known (CS_2) and an unknown (CS_3) underreporting period, and for interval-censored ($\beta_i = 2$) and right-censored ($\beta = \infty$) catches. Underreported landings are simulated according to scheme A.

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Table 2. Relative bias estimates in percentage for total catches (C), annual fishing rates (F), spawning stock biomass (SSB), and recruitment (R), based on 80 data sets for each combination of survey and catch CVs.

							CS_2						CS_3					
CV		ADAPT			CS_1			$\beta_2 = 2$			$\beta_2 = \infty$			$\beta_2 = 2$			$\beta_2 = \infty$		
Survey	Catches	P_1	P_2	P_3	P_1	P_2	P_3	P_1	P_2	P_3	P_1	P_2	P_3	P_1	P_2	P_3	P_1	P_2	P_3
C																			
0.8	0.2	–2	–29	1	–2	–28	1	1	4	1	3	7	5	15	8	21	15	10	25
0.8	0.072	–2	–27	1	–2	–25	–1	0	–7	–1	1	7	1	14	9	18	18	9	23
0.4	0.2	–2	–30	1	–2	–30	1	0	–3	2	0	–1	2	12	–8	16	16	–7	21
0.4	0.072	–2	–27	0	–2	–25	0	0	–6	0	0	–	1	13	–3	16	13	–4	20
0.2	0.2	–2	–29	1	–2	–29	–1	0	–4	1	0	–4	2	10	–9	13	13	–9	17
0.2	0.072	–2	–30	1	–2	–30	1	0	–7	1	0	–7	1	10	–4	14	11	–7	17
F																			
0.4	0.2	2	0	18	1	–1	16	–2	–1	12	–3	–1	13	0	–2	31	0	–2	33
0.4	0.072	2	0	17	1	0	15	–2	–2	13	–2	–1	14	0	–2	31	1	–2	32
0.2	0.2	1	0	16	1	–1	14	–2	–1	15	–1	–1	11	–1	–2	29	0	–1	32
0.2	0.072	1	4	18	0	3	16	–1	–2	12	0	–1	13	0	–1	27	1	0	29
0.05	0.2	1	–1	11	1	–1	10	–1	0	7	–1	–1	5	–2	–2	14	0	–1	15
0.05	0.072	1	–2	9	0	–1	9	0	0	6	0	–1	6	–1	–1	12	–1	–2	12
SSB																			
0.4	0.2	6	–12	–2	5	–11	–2	5	9	6	6	9	6	12	16	13	13	16	21
0.4	0.072	5	–12	–1	5	–11	0	5	8	6	5	7	5	12	15	12	13	15	18
0.2	0.2	4	–12	–1	3	–11	–1	4	4	3	4	4	4	6	5	11	7	5	13
0.2	0.072	4	–15	–4	4	–14	–4	5	4	2	5	5	3	5	5	8	6	6	12
0.05	0.2	2	–12	–2	2	–11	–1	3	4	2	3	4	2	4	5	8	5	5	10
0.05	0.072	2	–11	–3	2	–10	–2	1	3	2	2	3	2	3	4	7	6	4	9
R																			
0.4	0.2	4	–6	–3	4	–5	–3	7	6	9	7	6	10	10	9	19	12	11	22
0.4	0.072	3	–5	–2	3	–5	–1	7	5	8	7	6	9	9	8	16	11	10	19
0.2	0.2	3	–6	–1	2	–5	–1	4	4	5	4	5	5	6	6	7	7	6	7
0.2	0.072	4	–8	–2	4	–6	–2	5	4	4	5	5	4	6	4	6	6	5	6
0.05	0.2	4	–7	–1	4	–6	–1	4	4	4	5	4	4	5	5	6	5	6	7
0.05	0.072	2	–8	–2	3	–8	–1	3	4	4	4	5	3	5	4	6	5	4	7

Note: Findings are reported separately for the periods P_1 (1971–1984), P_2 (1985–1992), and P_3 (1993–2005). Results are presented for the uncensored ADAPT and CS_1 models, for models with a known (CS_2) and an unknown (CS_3) underreporting period, and for interval-censored ($\beta_2 = 2$) and right-censored ($\beta = \infty$) catches. Underreported landings are simulated according to scheme A.

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Table 3. RMSE (%) and relative bias (in parentheses) of total catch estimation over the complete period 1971–2005.

CV					CS_2		CS_3	
Survey	Catches	κ	ADAPT	CS_1	$\beta_y = 2$	$\beta_y = \infty$	$\beta_y = 2$	$\beta_y = \infty$
0.8	0.072	0.25	**16.8** (–4.7)	99 (–4.3)	154 (2.3)	204 (3.1)	255 (25.4)	258% (25.5)
		0.5	**26.6** (–7.7)	99 (–7.4)	82 (1.1)	141 (2.1)	162 (21.8)	165 (22.3)
		0.75	**33.8** (–9.9)	99 (–9.6)	51 (0.2)	122 (1.7)	135 (19.1)	138 (19.2)
0.4	0.072	0.25	**17.0** (–4.7)	98 (–4.4)	154 (–1.6)	159 (–1.5)	130 (18.5)	130 (18.8)
		0.5	**26.7** (–7.7)	99 (–7.4)	75 (–2.5)	80 (–2.3)	91 (16.8)	91 (16.9)
		0.75	**33.7** (–9.9)	99 (–9.6)	60 (–3.0)	72 (–2.7)	69 (15.2)	69 (15.5)
0.2	0.072	0.25	**16.9** (–4.8)	99 (–4.6)	80 (–2.6)	82 (–2.4)	92 (14.6)	92 (14.3)
		0.5	**26.6** (–7.8)	97 (–7.6)	65 (–3.4)	65 (–3.3)	66 (16.5)	67 (16.7)
		0.75	**33.7** (–10.0)	100 (–9.8)	58 (–3.8)	59 (–3.7)	53 (16.0)	54 (16.2)
0.8	0.2	0.25	**23.5** (–4.8)	100 (–4.5)	128 (2.6)	163 (3.4)	184 (25.5)	184 (25.6)
		0.5	**30.8** (–7.8)	98 (–7.6)	85 (1.0)	141 (2.7)	143 (21.9)	145 (21.8)
		0.75	**36.8** (–9.9)	99 (–9.7)	63 (–0.3)	127 (1.9)	126 (20.6)	129 (21.2)
0.4	0.2	0.25	**23.8** (–5.0)	99 (–4.6)	89 (–1.4)	91 (–1.2)	108 (19.7)	109 (19.9)
		0.5	**30.8** (–8.0)	100 (–7.6)	76 (–2.6)	78 (–2.1)	83 (17.1)	83 (18.0)
		0.75	**36.9** (–10.0)	100 (–9.7)	65 (–3.0)	66 (–2.5)	67 (16.2)	69 (16.4)
0.2	0.2	0.25	**23.7** (–5.0)	100 (–4.8)	83 (–2.2)	84 (–2.0)	84 (19.6)	84 (19.6)
		0.5	**30.8** (–8.1)	98 (–7.9)	69 (–3.4)	71 (–3.1)	68 (17.9)	72 (18.4)
		0.75	**36.9** (–10.2)	100 (–10.0)	62 (–3.8)	63 (–3.6)	58 (18.1)	61 (18.2)

Note: ADAPT RMSEs are in bold type. Relative RMSEs with respect to ADAPT RMSEs, in percentage, are given in Roman type. Results are presented for the uncensored ADAPT and CS_1 models, for models with a known (CS_2) and an unknown (CS_3) underreporting period, and for interval-censored ($\beta_y = 2$) and right-censored ($\beta = \infty$) catches. Underreported landings are simulated according to scheme B, indexed by κ.

well as the estimation of the catches under scheme B (Table 3). The censored FA models did not give reasonable estimates of SSB, R, and F for a survey CV of 0.8; these results are not presented. In a similar way, the censored FA models estimated the catches very well, with a survey CV of 0.05; these are omitted. Thus, three survey CVs are considered for each set of parameters.

ADAPT and CS_1 estimates always have similar properties. They perform reasonably well when there is little or no underreporting. Even if CS_1 allows observation errors, it does not do better than ADAPT. The CS_2 model, with $\beta_y = 2$, gives the best results for both bias and RMSE among all censored models. For estimating catches (C) and fishing mortality rates (F), it also outperforms ADAPT and CS_1. For both CS_2 and CS_3, the estimates obtained with $\beta_y = \infty$ have larger RMSEs, especially in the most extreme case where the survey CV = 0.8 and the catch CV = 0.072. However, in general, going from $\beta_y = 2$ to $\beta_y = \infty$ when estimating the parameters does not change the results much.

Model CS_3 performs better than both ADAPT and CS_1 for catch estimation in the period of underreporting, except when the survey CV is 0.8. However, the CS_3 model is sensitive but not specific: if there is underreporting, it will flag it, but it can show underreporting in years when there is none. Note also that CS_2 outperforms ADAPT and CS_1 in bias and RMSE for estimating SSB_y in the period of underreporting if the survey CV is at most 0.2.

Large biases have been highlighted (Table 2). In all of the models, the absolute abundance estimates SSB and R are driven by the catches. The uncensored model underestimates both in the years of underreporting. Allowing censored catches gives larger SSB and R values; thus, all the censored models overestimate SSB and R. All of the models overestimate the fishing mortality rates in the third period. This might be an artefact of the small size of the stock in that period. The SGSL cod stock has an estimated survey CV of 0.63; thus, the censored FA model is unlikely to yield better estimates of the age-specific abundances $N_{a,y}$ and of SSB and R than the ADAPT or the uncensored FA model.

To check the ability of Z_y given by eq. 15 to detect underreported catches, we displayed yearly box plots of the 80 replicates of this statistic obtained with the CS_3 model with $\beta_y = 2$, for data sets generated with a survey CV of 0.4 and a catch CV of 0.072 (Appendix A, Fig. A2). The break points between 1985 and 1992 are clearly visible. This agrees with the results obtained in the SGSL case study. The lack of specificity noticed earlier shows up in this plot: all the Z_y values are positive and suggest some small underreporting at the beginning and end of the observation period.

Results on the estimation of the catches when the censoring scheme used for the simulation differs from the scheme used for the estimation are given (Table 3). Model CS_2 provides nearly unbiased catch estimates, even if the survey CV is large. The censored model appears to be robust to the specification of the censoring mechanism for estimating catches. Indeed, the RMSEs and the biases of ADAPT and the CS_1 model are higher than those of the censored models, except when $\kappa = 0.25$ (Table 3). Note that in the latter case, the landings are close to the true catches. Even if it overestimates the catches by 10% to 20%, model CS_3 outperforms both ADAPT and CS_1 in most cases, provided that the survey CV is equal to or lower than 0.4. In addition, when the survey CV is under 0.8, taking $\beta_y = 2$ and $\beta_y = \infty$ yields similar results. Thus, the subjective selection of a β_y value can be avoided by systematically taking $\beta_y = \infty$.

Discussion

In this article, we extended the censoring of catches introduced by Hammond and Trenkel (2005) to age-structured

models. We considered the true catches as unknown model parameters and landings as lower bounds for noisy catch measurements. We built a model for the SGSL cod stock and showed, through a simulation study, that it can reconstruct the true catch history when the landings are underreported.

This approach involves two steps. From simulations based on a real case study, we showed that crudely censored likelihoods are able to detect underreported catches when the natural mortality is assumed known. Full-censored strategies are diagnostic tools. Once problematic catches are identified, additional information can be sought to determine a more precise censoring scheme. This can lead to improved estimation of the true catches. We also succeeded in getting catch estimates that are better, in mean squared error, than simulated landings and uncensored estimates. Even when the model for the censoring of the landings is incorrect (scheme B), censored methods still provided reliable estimates.

Extensions of the model

We developed a model suitable for the SGSL cod stock assessment. In the rest of this section, we outline some generalizations that could make the model useful for other stocks.

First, for long-lived and not intensively fished species, approximation (eq. 8) is inappropriate and can be replaced by the standard plus-group equation:

$$N_{A,y+1} = N_{A,y}\exp(-Z_{A,y}) + N_{A-1,y}\exp(-Z_{A-1,y})$$

Second, the $I^*_{a,y}$ likelihood assumed that the estimated indices were all independent. A more realistic model might have correlated survey indices within years, as discussed in Myers and Cadigan (1995). This only impacts the survey likelihood. Following Chassot et al. (2009), one then has to define one likelihood term for the total survey indexes (summed over ages) and another term for the proportions at age in the population. In addition, the behavior of the proposed censored FA model when $I^*_{a,y}$ are missing for some values of a or y should be investigated.

Another important issue is age-specific underreporting, which can be due to highgrading. This can be accommodated by partitioning the age classes into two sets — one with misreporting (set 1) and one without (set 2). The likelihood would then be written in terms of the yearly landings in the two sets, $L^{*(1)}_y$ and $L^{*(2)}_y$. Censoring is included only for $L^{*(1)}_y$.

The assumption of known values of $\rho_{a,y}$ could be relaxed by adding a term to the likelihood for the estimation of these parameters using either the landings-at-age data or some biological sampling data. Likelihoods for complex sampling schemes used for size and age information (i.e., length-stratified age samples, cluster samples) are complex, and in practise, simple approximations are used (e.g., Quinn and Deriso 1999).

The treatment of the natural mortality rate M could also be refined. If the real natural mortality rates are suspected to exceed the fixed values chosen in this paper, a part of the estimated catches may actually represent natural deaths, which should be removed before correcting the landings. Therefore, preliminary studies must be made to provide reliable estimates of M using survey data, as in Sinclair (2001). Otherwise, a separability assumption may probably be necessary to estimate M.

Finally, terms can be added to the likelihood to account for other sources of uncertainty in the assessment method. Each additional term makes the likelihood maximization more complex. More complicated models could be implemented in a Bayesian framework, where computer-intensive estimation methods can be used for parameter estimation. One interest of the relatively simple model that we proposed for the SGSL cod stock is the ability to carry out inference in a standard frequentist framework, which might be preferable when sources of reliable prior information are unavailable, as might be the case in stock assessment.

Comparison with other methods and future work

The censored approach may provide advantages when compared with alternatives for population modelling and catch correction such as the BADAPT model (Darby 2005). The latter model requires a time period of reliable catch data and survey data that overlap the period of reliable catch data and the period in which misreporting occurs. The censored FA model only requires crude bounds on the true catches. This is especially interesting for modelling many species with large historic catches for which important misreporting was unlikely for many years, because it was not possible to blackmarket or discard large amounts of catch. These years can be given β values only slightly larger than 1.

The relatively poor performance of the censored FA model when estimating management parameters needs further investigation. The solution might be to use simultaneously several abundance indices and also to constrain interannual variations in fishing mortality within realistic values, perhaps using a random walk approach.

Changes to the estimation procedure itself could also be investigated. Alternatives to the SA algorithm could be considered. The threshold acceptance strategies of Dueck and Scheuer (1990) could improve its convergence. In addition, adapting the SA algorithm to assessment models that feature a random process error is a challenging problem. The advances proposed by Andrieu and Doucet (2000) and de Valpine and Hilborn (2005) seem promising in this regard.

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Appendix A

Cubic spline catchability function

The cubic spline function $Q(\cdot|\delta)$, chosen to structure the catchability at age, can be described as follows: between the knots defined as ages (0, 1, …, A), A piecewise three-degree polynomials $Q(\cdot|\delta) = Q_0(\cdot|\delta), \ldots, Q_{A-1}(\cdot|\delta))$, of total dimension $\dim(\delta) = 4A$, are fitted under the following constraints:

1. interpolating constraints: $Q(0|\delta) = 0$, and for $a = 1, \ldots, A$,

$$\text{(A1)} \qquad Q(a|\delta) = \frac{\sum_{y=1}^{Y} I^*_{a,y}}{\sum_{y=1}^{Y} N_{a,y}(\mathbf{C},\mathbf{S})}$$

2. twice continuity and differentiability constraints: for $a = 1, \ldots, A-1$,

$$Q_{a-1}(a \mid \delta) = Q_a(a \mid \delta)$$

$$Q^{(i)}_{a-1}(a|\delta) = Q^{(i)}_a(a|\delta) \quad \text{for } i \in \{1, 2\}$$

Table A1. Estimated cod survivors (N_a, tonnes) in 2005 and catchabilities (Q_a).

Age a	$N_{a,Y}$	Q_a
1	9 023	7.543×10^{-5}
2	17 266	1.833×10^{-4}
3	15 344	2.712×10^{-4}
4	10 355	3.440×10^{-4}
5	7 211	3.949×10^{-4}
6	5 922	3.807×10^{-4}
7	5 479	3.983×10^{-4}
8	4 719	3.783×10^{-4}
9	3 091	4.165×10^{-4}
10	1 256	4.648×10^{-4}
11	316	4.514×10^{-4}
12	515	7.152×10^{-4}
13	325	9.703×10^{-4}
14		1.246×10^{-3}

Note: Numerical age a represents biological age $a + 1$.

The interpolating points (eq. A1) have been chosen to reduce the influence of yearly trends on the age structure of the catchability. The choice of a cubic spline ensures smoothness and minimizes the interpolating oscillations under the supplementary constraint $Q''(1|\delta) = Q''(A|\delta) = 0$, which is required by a classic logistic form of the selectivity at age (Harley and Myers 2001) and appears necessary to ensure the determination of polynomial parameter vector δ (Hastie 1992).

The SA algorithm

The principle of the SA algorithm is to maximize the function $f_T(\theta) = \exp(l^p(\theta)/T)$, where $l^p(\theta)$ is the profile log-likelihood (eq. 14), and for which $T > 0$ decreases towards 0 in successive steps. Indeed, $f_T(\theta)$ becomes concentrated around the MLE $\widehat{\theta}$. Denote by θ_i and T_i the estimate of $\widehat{\theta}$ and the value of T at step i (θ_0 being the value obtained with Nelder–Mead's method). Following Pibouleau et al. (2005), a practical value for T_0 is $|l^p(\theta_0)|$. To obtain a fast method, a geometric rate of $T_i = 0.99^i T_0$ is often chosen for practical implementation. To explore the MLE region and avoid possible local maxima, the renewal of θ_i at step i is made following a Metropolis procedure (Robert and Casella 2004): a new value of θ_i is sampled from an instrumental distribution $\pi(\theta|\theta_{i-1})$. It is accepted or refused according to its probability of increasing $f_T(\theta)$ with respect to θ_{i-1}: the larger the probability, the closer we are from the MLE. In our case, $\theta = (\mathbf{C}, \mathbf{S})$ and $\pi(\theta|\theta_i)$ is chosen as a truncated multivariate normal distribution $\mathcal{N}(\theta_i, \Sigma_i)$, discretized on $\mathbb{N}^{A-1+Y}$. Lower bounds are 0, and upper bounds have been set to five times the reported landings and the ADAPT estimates of survivors. Indeed, instrumental sampling on finite state–space ensures the convergence of the SA chains to $\widehat{\theta}$ (Hàjek 1988; Winkler 1995). The instrumental variance Σ_i has been chosen as $\lambda_i \theta_0 \mathbf{I}$, where $\mathbf{I}$ is the identity matrix on $\mathcal{R}^{A-1+Y}$ and where the one-dimensional coefficient λ_i is empirically calibrated at each step to ensure an acceptance rate of 25% during the first 2000 iterations (λ_i is increased or de-

Fig. A1. Reconstitution of catch histories using 11 various censoring schemes placed on real SGSL cod landings (circles). Two schemes consider all reported landings as censored random values, with $\beta_y = 2$ and $\beta_y = 1.5$. Two schemes consider only the period 1971–1992 as censored, with $\beta_y = 2$ or $\beta_y = 1.5$. Two schemes consider the years 1985–1992 and 2003–2005 as censored, with $\beta_y = 2$ or $\beta_y = 1.5$ for the first period and $\beta_y = 1.25$ for the second period. Two schemes consider the years 1971–1992 and 2003–2005 as censored, with $\beta_y = 2$ or $\beta_y = 1.5$. Two schemes consider the period 1985–1992 and the year 2003 as censored, with $\beta_y \in \{2, 1.5, \infty\}$ for 1985–1992 and $\beta_y = 1.25$ for 2003. Finally, one scheme considers three time periods of censoring: years 1985–1992, 1993–1998, and 2003, with $\beta_y = 2$, 1.25, and 1.25, respectively.

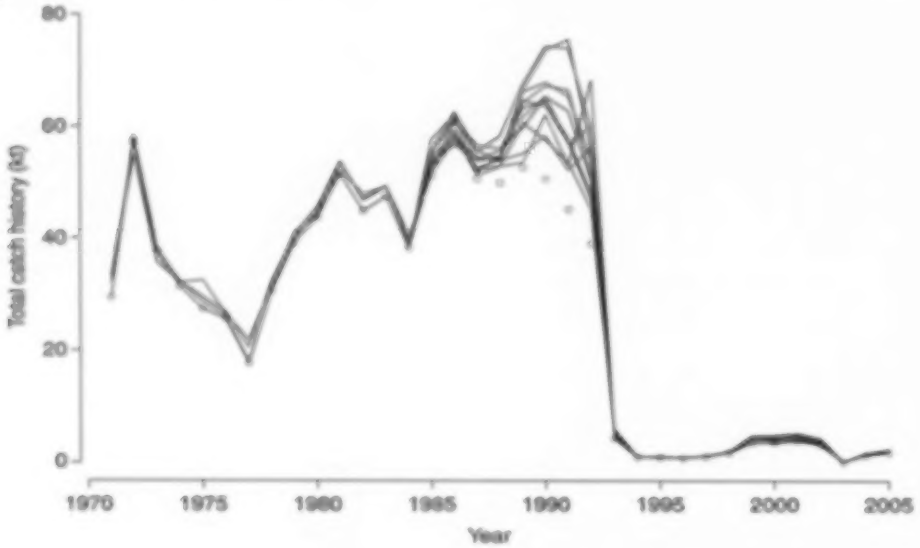
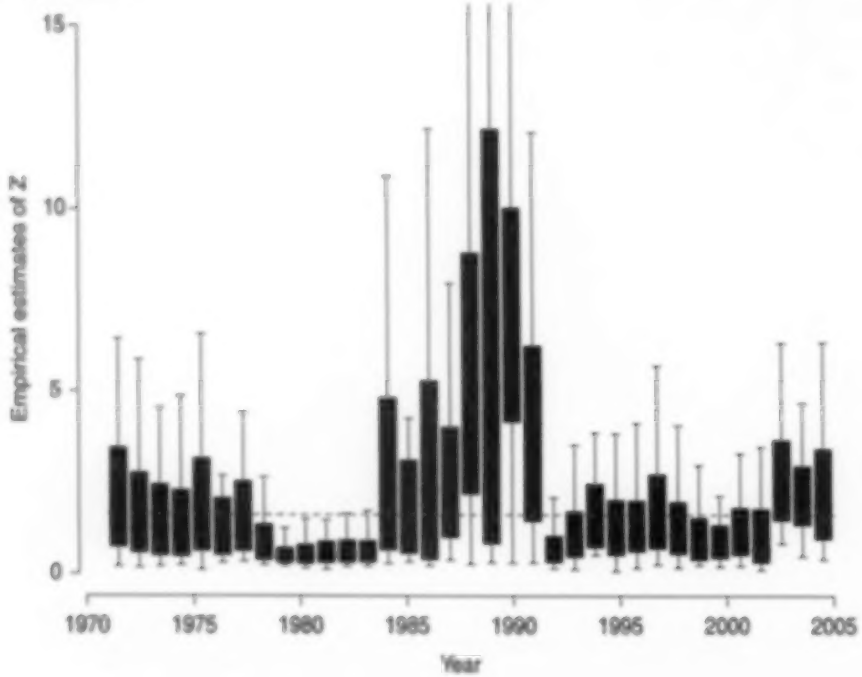


Fig. A2. Box plots of values Z_y estimated by the full-censored FA model with $\beta_y = 2$, based on 80 independent data sets with underreported catches simulated according to scheme A. The survey CV is 0.4 and the catch CV is 0.072. The horizontal broken line indicates the 95%-order standard normal percentile 1.645.



creased such that four steps are necessary, on average, to select a new value of θ). This value has been recommended by Roberts et al. (1997) for high-dimensional models. The choice of a diagonal Σ_i does not take into account the possible correlation between the parameters. Finally, the SA scheme can be summarized as follows.

Simulated annealing algorithm

Step 0: let θ_0 be a Nelder–Mead estimate of $\widehat{\theta}$ and select $T_0 = |\ell^p(\theta_0)|$.

Step i:

1. sample $\tilde{\theta}$ from $\pi(\theta|\theta_{i-1})$;
2. accept $\theta_i = \tilde{\theta}$ with probability $\min(1, \exp(\{\ell^p(\tilde{\theta}) - \ell^p(\theta_{i-1})\}/T_{i-1}))$;
3. update $T_i = 0.99\,T_0$.

Stop when θ_i remains nearly unchanged after several iterations of T_i.

The approximate SA distribution was produced using the principle of importance resampling, which became very popular in Bayesian analysis (Rubin 1988). This was carried out from exploration data generated by the addition of a random local exploration step to the classic SA algorithm. On average, we experimented with 1500 iterations before reaching stability of the estimation. By switching the SA algorithm to a random walk with a small coefficient of variation (10%), we got 500 different values close to the stable estimation. We then considered the cloud of the last 1000 points as a good set of values with which to explore the area of the MLE. Then we (*i*) computed the values of the corresponding likelihood and renormalized them between 0 and 1 to get probabilities and (*ii*) resampled the catch estimates, with replacement, according to the multinomial distribution defined by these probabilities. This step is necessary to zoom in on the MLE area.

There are, of course, identical and correlated values in the final set of estimates, but this does not differ from any posterior Bayesian approximation obtained by common MCMC or importance sampling approaches. Variances and confidence intervals were finally estimated by selecting randomly 250 vectors from among the 1000 resampled ones. This crude heuristic (following Rubin 1988) allowed the influence of correlations to be diminished. The wider the range of estimates, yielding close likelihoods, the larger is the variance of the MLE.

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Phosphorus and land-use changes are significant drivers of cladoceran community composition and diversity: an analysis over spatial and temporal scales

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Abstract: We conducted paleolimnological studies over spatial and temporal gradients to define the responses of subfossil cladoceran community composition and diversity to changes in land use and phosphorus concentrations in shallow lakes. We predicted that watershed disturbance by humans, through its impact on water quality, would explain significant variation in cladoceran diversity and composition. Across lakes, water-column total phosphorus concentration was a significant ($p < 0.05$) predictor of the subfossil cladoceran community composition. Chydorid diversity was also found to be related significantly to phosphorus concentration ($r = -0.55$, $p < 0.05$) and the proportion of disturbed land in the watershed ($r = -0.47$, $p < 0.05$). However, net load of phosphorus to the watershed rather than proportion of watershed disturbance was a significant predictor of chydorid diversity ($r = -0.86$, $p < 0.001$) in our temporal analysis of an eutrophying lake. Given that phosphorus loading to surface waters is often related to phosphorus concentrations in soils, we suggest that the net phosphorus load to the watershed is a more sensitive metric of land-use change and necessary for detecting ecological responses in time series data.

Résumé : Des études paléolimnologiques le long de gradients spatiaux et temporels nous ont servi à définir les réactions de la composition et de la diversité de la communauté subfossile de cladocères aux changements d'utilisation des terres et de concentrations de phosphore dans des lacs peu profonds. Nous avons prédit que la perturbation des bassins versants par les humains, par son impact sur la qualité de l'eau, expliquerait une partie importante de la variation de la composition et de la diversité des cladocères. Dans l'ensemble des lacs, la concentration de phosphore total dans la colonne d'eau est une variable prédictive significative ($p < 0,05$) de la composition de la communauté subfossile de cladocères. La diversité des chydoridés est aussi reliée significativement à la concentration de phosphore ($r = -0,55$, $p < 0,05$) et à la proportion de terres perturbées dans le bassin versant ($r = -0,47$, $p < 0,05$). Cependant, dans notre analyse temporelle d'un lac en voie d'eutrophisation, la charge nette de phosphore dans le bassin versant, plutôt que le pourcentage de perturbation du bassin versant, est une variable prédictive significative de la diversité des chydoridés ($r = -0,86$, $p < 0,001$). Étant donné que la charge de phosphore vers les eaux de surface est souvent reliée aux concentrations de phosphore dans le sol, nous croyons que la charge nette de phosphore vers le bassin versant est une métrique plus sensible au changement d'utilisation des terres et qu'elle est nécessaire pour détecter les réponses écologiques dans les séries chronologiques de données.

[Traduit par la Rédaction]

Introduction

Nutrient enrichment of freshwaters is one of the most widespread forms of anthropogenically induced global change (Carpenter et al. 1998; Tilman et al. 2001). Elevated loading of nutrients to shallow lakes, mainly in the form of phosphorus and nitrogen, results in increased phytoplankton biomass and decreased water clarity, which in turn can fundamentally alter lake food webs (e.g., Scheffer et al. 1993, 2001; Vadeboncoeur et al. 2008). Since the 1970s, many governments have regulated the discharge of nutrients to surface waters, but non-point sources in the form of runoff from agricultural and urban areas continue to be a major source of nutrients to lakes (Carpenter et al. 1998; Bennett et al. 1999). A current focus of eutrophication research is to define the interactions among land use – land cover, water quality dynamics, and aquatic community structure (e.g., Gélinas and Pinel-Alloul 2008). To date, this research has largely been focused on lake survey analyses (Hoffmann and Dodson 2005). However, it is not yet clear whether we can assume that biodiversity patterns derived over spatial

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gradients can be used to predict what might occur within a single lake over time (Dodson et al. 2000). We believe that comparative paleolimnological and land use – land cover analyses, which can be conducted across both spatial and temporal gradients, are particularly insightful as they can allow investigators to fully evaluate how applicable results are across these different scales.

Subfossil cladoceran assemblages provide valuable insight into how eutrophication has altered the structure and functioning of aquatic systems (e.g., Frey 1960; Manca et al. 2007). In particular, planktonic Cladocera play a key role in controlling phytoplankton biomass as they actively graze small-sized phytoplankton and sequester limiting nutrients from ungrazed algae (Sommer and Sommer 2006). Furthermore, the community structure of the littoral Cladocera (i.e., chydorids) is known to be very sensitive to changes in nutrient levels (e.g., Whiteside 1970; de Eyto et al. 2003) and macrophyte coverage (e.g., Quade 1969; Duigan and Kovach 1994). Planktonic and littoral cladoceran communities differ, however, in their sensitivities to fish predation where the community structure of planktonic taxa is more strongly controlled by planktivory pressure (Jeppesen et al. 1996).

In this study, we first conducted paleolimnological analyses across a spatial gradient (i.e., an among-lake surface sediment survey) to define the nutrient autecologies of cladoceran taxa in northeastern North American shallow lakes. We predicted that nutrients (total phosphorus (TP)) and factors related to habitat quality (e.g., depth and turbidity) would explain a significant amount of variation in the cladoceran community structure. We then conducted a detailed lake study and used the results from the spatial analysis to interpret the sediment core data so that we could define the lake's responses to land-use change.

A second objective of this paper was to test the generality of a principle proposed by Dodson et al. (2007), who suggested that watershed land use, through its impact on water quality, was a key factor structuring zooplankton diversity and composition in field settings. Dodson et al.'s (2005, 2007) research was based on a large spatial survey of pelagic zooplankton from 73 lakes. Here we use paleolimnology, land use, and historical census data to evaluate this principle over spatial and temporal gradients. To our knowledge, the relationship between watershed land use and cladoceran diversity and composition in shallow lakes has not been tested quantitatively over a centennial time scale.

Materials and methods

Study sites and paleolimnological analyses

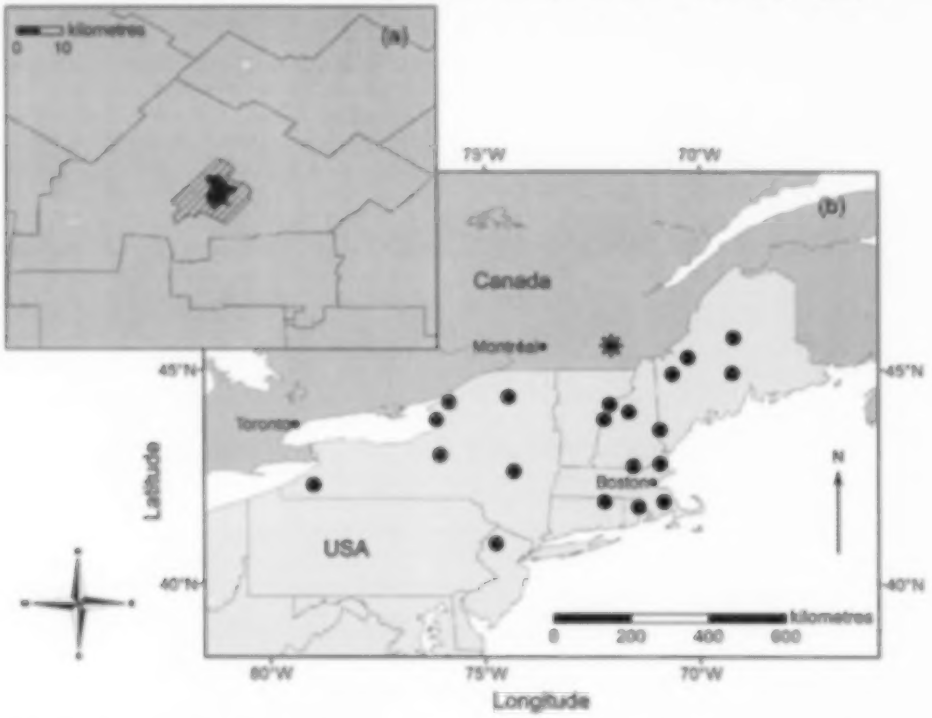
The Environmental Monitoring and Assessment Program (EMAP) has created a valuable database that includes physicochemical and environmental data for 257 randomly selected northeastern North American lakes (available from www.epa.gov/emap/). A subset of 20 randomly selected, primarily shallow lakes (i.e., Z_{mean} = 3.2 ± 2.8 m, mean ± standard deviation (SD)), spanning a large phosphorus gradient (mean TP = 0.9–154.5 $\mu g \cdot L^{-1}$) was included in our surface sediment analysis (Fig. 1; for a more complete limnological description, see Appendix A, Table A1). Surface sediments from each lake were collected using a gravity corer (see Dixit et al. 1999). We analysed the top 0–1 cm of each sediment core, which represents an integrated sample of the entire lake's production over the past ~1–4 years (Smol 2008).

We also conducted a detailed analysis of a sediment core from a shallow lake in northeastern North America to reconstruct the response of cladocerans to environmental change over the past ~150 years (Fig. 1). Petit Lac Saint-François (aka Tomcod Lake) is a hypereutrophic (mean summer TP = 193 $\mu g \cdot L^{-1}$) shallow lake (Z_{mean} = 0.9 m) that flushes quickly (water residence time of 0.06 years). The phytoplankton of Petit Lac Saint-François is dominated by cyanobacteria (I. Gregory-Eaves, personal observation) and was found to have the highest epilimnetic microcystin concentrations relative to other lakes in the region (Giani et al. 2005). The lake is set within a relatively large, but gently sloping, watershed that is underlain by sedimentary bedrock (mean catchment slope = 2.5% and drainage area – lake area ratio (DA:LA) = 24). A sediment core was retrieved from the deeper portion of the lake using a modified Kajak–Brinkhurst gravity corer (Glew 1989). The core was subsampled in the field at 1 cm resolution using a vertical extruder (Glew 1988). Samples were freeze-dried and processed for ^{210}Pb dating. The radioisotope activities of ^{210}Pb, ^{214}Pb, and ^{214}Bi from a known mass (0.4 to 1 g) and volume of freeze-dried sediment were measured for 24 h using a Canberra well-detector gamma ray spectrometer. Sediment ages were calculated using the constant-rate-of-supply (CRS) model (Binford 1990). Based on the derived sedimentation rates, we calculated fluxes (aka the accumulation rate of remains per defined area and time period, i.e., a standardized paleolimnological indicator of production) for several cladoceran groups to take into account differences in sedimentation rates between samples.

Counts and identifications of cladoceran remains were done using a Leica DM2500 compound microscope (200–400× magnification) with the aid of taxonomic keys (Frey (1985), Smirnov (1996), and Bos (2000) and references cited therein). All remains were identified down to the lowest possible taxonomic level. *Daphnia* were identified to the species group level (*D. pulex* and *D. longispina* groups), and *Bosmina* and chydorids were identified to the species level when possible. Following standard methods, we adjusted counts of remains to be representative of the cladoceran population as individuals are comprised of two halves forming the carapace, one headshield and one postabdomen, which are often found separately (Korhola and Rautio 2001). The most abundant remain is used to represent each individual until at least 60 individuals of the chydorid group have been counted (Frey 1986).

To describe the geochemical changes of the sediment core collected from Petit Lac Saint-François, we conducted measurements of loss-on-ignition at 550 °C (LOI 550; Heiri et al. 2001) and magnetic susceptibility (Sandgren and Snowball 2001). The LOI 550 measurements describe the changes in the relative amount of organic matter (vs. inorganic matter) across the core. Magnetic susceptibility measurements quantify the relative abundance of magnetic minerals present in the sample (e.g., iron and manganese carbonates), which are often transported to a lake via catchment erosion (Sandgren and Snowball 2001).

Fig. 1. Maps of our study sites: (*a*) high spatial resolution map showing the delineation of the Petit Lac Saint-François watershed (black) set within the smaller census subdivision (hatched) and the larger census division boundaries (lines); (*b*) map of the northeastern US and southeastern Canada showing the location of the EMAP study sites (solid circles) and Petit Lac Saint-François (star).



Quantifying land-use change in the Petit Lac Saint-François region

To define land-use changes in the region surrounding Petit Lac Saint-François, we compiled agriculture and population census data from the Government of Canada dating from the earliest periods available (i.e., 1851 for human population and 1871 for agriculture) until 2001 (Canada Department of Agriculture 1851, 1861, 1873, 1883, 1893, 1901; Canada Census and Statistics Office 1911; Canada Dominion Bureau of Statistics 1922, 1932, 1942, 1952, 1962; Statistics Canada 1972, 1982, 1992, 2003). Data on the extent of cropland and pastureland, as well as human population trends, were available at both census division (coarse) and census subdivision (fine) scales (Fig. 1). The historical agricultural census data includes inventories of annual fertilizer purchases, livestock numbers, and crop production. We used these data to estimate the amount of phosphorus (P) fertilizer and livestock manure P applied to croplands in this region historically, as well as the P removed by harvested crops (see MacDonald and Bennett 2009). Specifically, we defined changes in the regional P budget (i.e., net P load to the watershed soils, a metric of agricultural intensity) as the difference between annual P inputs (fertilizer P and P derived from livestock manure, kg $P \cdot ha^{-1} \cdot year^{-1}$) and P removed in harvested crops (kg $P \cdot ha^{-1} \cdot year^{-1}$). The regional P budget was calculated at the census division scale because fertilizer and livestock density data were available only at this scale over most of the study period. We found, however, that time series data on the extent of cropland at the census division and subdivision scales were significantly correlated ($r = 0.80$, $p = 0.001$, $n = 13$), which suggests that the census division data accurately tracked temporal trends in land use at both spatial scales.

Statistical analyses

Surface sediment analyses

We first conducted a series of ordination analyses to define both qualitatively and quantitatively the relationships between environmental variables and modern sedimentary cladoceran assemblages. Cladoceran species that were present in at least two sites at >2% relative abundance were used in all ordinations. Species data were square root transformed to reduce the influence of dominant taxa and stabilize the variation. We first applied detrended correspondence analysis (DCA) to quantify the length of gradient represented by our surface sediment samples. Given that this preliminary analysis revealed a relatively short gradient length (i.e., 0.95 SD units), we subsequently applied linear ordination techniques (Lepš and Šmilauer 2003).

Redundancy analysis (RDA) was performed to quantify relationships between the full cladoceran assemblages and measured physical and environmental variables (chlorophyll *a*, colour, conductivity, dissolved organic carbon, dissolved inorganic carbon, TN, TP, pH, turbidity, mean depth, lake surface area, lake volume, percent watershed disturbance) (Appendix A, Table A1). All values were either square root or natural log transformed to generate nor-

malized distributions. Prior to running the RDA with forward selection, however, we identified collinear variables with a Pearson's correlation and only included one of the variables from a correlated group (i.e., $r > 0.8$) in our RDA (Lepš and Šmilauer 2003). Specifically, the variable that explained the most variation in the cladoceran assemblage when run as a single variable in a preliminary RDA was included in the final RDA. All ordination analyses were performed using CANOCO software (version 4.5; ter Braak and Šmilauer 2004).

To quantify subfossil cladoceran diversity within our sediment samples, we applied two metrics: Simpson's diversity index (Simpson 1949) and rarefied species richness estimates (Hurlbert 1971). For both metrics, we calculated diversity exclusively within the chydorids because this is a species-rich group that is known to preserve well in lake sediments (Korhola and Rautio 2001). For the species richness estimates, we applied rarefaction to standardize chydorid counts to 60 individuals. All diversity metrics were calculated using the "vegan" package in the statistical program R (R Development Core Team 2007).

Correlation analyses were run to assess the strength of the relationship between chydorid species richness estimates and TP, the proportion of disturbed watershed area (i.e., percent disturbance, which is the sum of percent agricultural land and percent urban land), or lake surface area. Lake surface area, TP, and species richness data were log-transformed, and percent disturbance data were arcsine square root transformed to normalize distributions. Correlation analyses were performed using JMP (version 7; SAS Institute Inc. 2007). We also verified whether there was significant spatial autocorrelation in any of our variables to ensure that our correlation p values were not artificially low. Following methods similar to those of MacDonald and Bennett (2009), we used OpenGeoDa for Windows (version 0.9.8.14; GeoData Center for Geospatial Analysis and Computation, Tempe, Arizona) to test for spatial dependence in the variables listed above but failed to detect any strong or significant spatial effects (based on interpretation of Moran's I or Lagrange multiplier values, where appropriate, all with $p > 0.05$).

Sediment core and historical analyses

We used correlation analyses to quantify the strength of the relationship between land-use metrics based on our census data collection and the flux of different cladoceran groups or chydorid diversity. Prior to running correlation analyses, the normality of all variables was assessed. $\text{Log}(x + 1)$ transformation was applied to LOI 550 data, as well as to *Bosmina*, *Daphnia*, and chydorid flux data.

Similar to our spatial analyses, we conducted an assessment to evaluate whether there was significant autocorrelation in our time series data that could bias correlation p values that were derived from statistical tables. We detected significant lag-1 correlations for all time series data and thus followed the approach outlined in Keller et al. (2008). In particular, we conducted a randomization test to calculate a p value for each set of covariates. We first created 9999 randomly reshuffled time series of one of our variables (e.g., *Bosmina* flux) and then correlated each of these time series with a nonrandomized time series (e.g., net P load to the watershed) such that we had calculated 9999 correlation coefficients for each set of covariates. The p value was then calculated as the number of randomization-based correlations plus the observed correlation that were equal to or larger than the observed correlation, divided by the total number of correlations (i.e., the number divided by 10 000). We also adopted a conservative alpha level for our temporal analyses where only p values < 0.01 were considered significant.

For our diversity analyses, we followed the same approach as described above in the spatial survey, but with two exceptions. We presented species-richness profiles from the sediment core samples based on individual samples, as well as on integrated samples that represent similar time intervals. This latter step was taken to address the issue raised by Smol (1981), who cautioned that alpha diversity indices (i.e., species richness) need to account for changes in sedimentation over the course of paleolimnological records to provide an unbiased perspective of change over time (i.e., sediment intervals from different parts of the core may be integrating different amounts of time, which could have an impact on diversity estimates). For the integrated sample profile, we pooled data across equally spaced time steps (i.e., 20–30 years) and then conducted rarefaction on these pooled samples. Rarefaction of the sediment core samples was standardized to chydorid counts of 60 individuals.

We also conducted an RDA analysis in which we plotted the fossil samples (i.e., core samples from Lac Petit Saint-François) passively in the ordination space based on the surface sediment and associated environmental data from the spatial lake survey. The goal of this analysis was to show the trajectory of change in the core samples relative to the environmentally defined axes of cladoceran community composition collected over a broader spatial scale.

Results

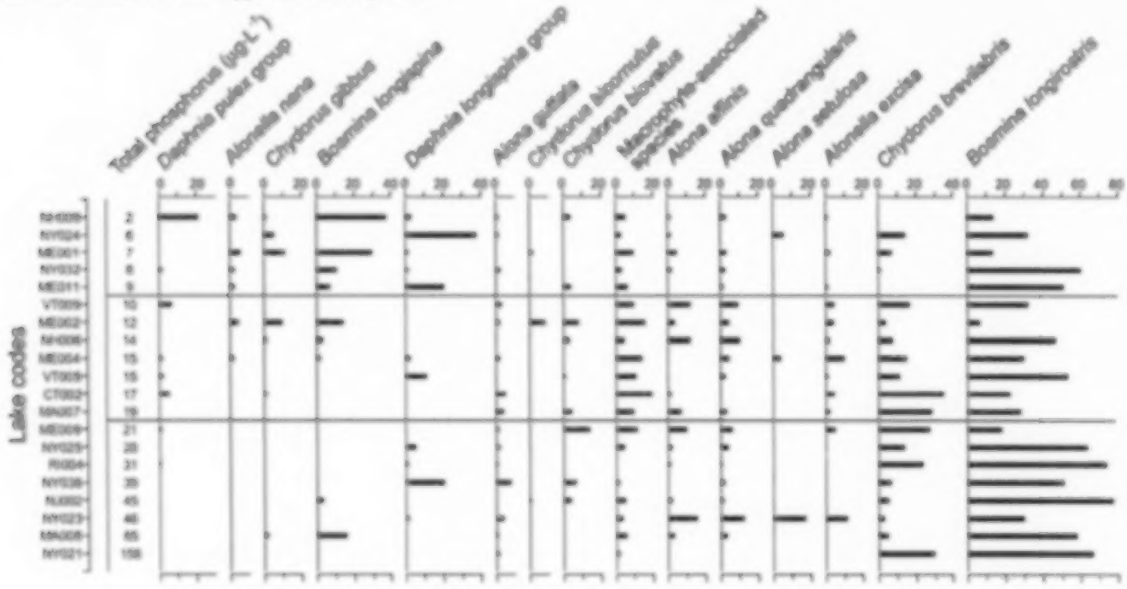
Modern spatial survey

A total of 50 Cladocera taxa were identified in the 20-lake EMAP data set. Of these, 35 taxa had >2% abundance in at least two different sites and were included in ordination analysis (Appendix B, Table B1). *Bosmina longirostris* was the most abundant taxon, occurring in all lakes with a relative abundance of 41.2% ± 2.14% (mean ± SD). The remaining assemblage was largely comprised of the predominantly littoral Chydoridae family (mean relative abundance 44.1% ± 1.08%) of which *Chydorus brevilabris* was dominant (mean relative abundance of 12.6% ± 2.13%).

The RDA, with forward selection, of the surface sediment cladoceran community assemblages identified three significant ($p < 0.05$) environmental predictors: TP, pH, and mean depth. Total phosphorus explained the largest portion of the variation (13.3%) in the cladoceran assemblages. TP was also highly correlated with chlorophyll a ($r = 0.82$, $p < 0.01$) and turbidity ($r = 0.82$, $p < 0.01$). pH and mean depth explained a further 12.7% and 9.8%, respectively, of the variation in the modern cladoceran assemblages.

Across a large TP gradient, it is clear that there are specialist taxa that are abundant within a fairly narrow TP range, whereas others are more broadly distributed (Fig. 2). For example, the *Daphnia pulex* group, *Alonella nana* and *Chydorus gibbus*, were primarily found in oligotrophic to

Fig. 2. Cladoceran species assemblages found in surface sediments from 20 northeastern North American EMAP lakes (data are expressed as percent relative abundance). Only taxa that were present in greater than 5% are shown. Lake trophic status is categorized based on total phosphorus (TP) measurements. Note that the taxa included in the macrophyte-associated group are *Alona rustica*, *Alona intermedia*, *Eurycercus lamellatus*, *Pleuroxus* spp., and *Sida crystallina*.



mesotrophic waters. Conversely, the dominant *Bosmina longirostris* was present across the entire gradient but showed increased relative abundance at higher TP levels. *Chydorus brevilabris* was also a taxon with a widespread distribution (present in 19 of the 20 sites) but occurred at higher relative abundances in mesotrophic to hypereutrophic waters. Macrophyte-associated taxa (a group comprised of *Alona rustica*, *Alona intermedia*, *Pleuroxus* spp., *Eurycercus lamellatus*, and *Sida crystallina* (Smirnov 1996)) were most abundant in mesotrophic sites.

With both the Simpson's and species-richness estimates of diversity, we found that chydorid diversity was negatively correlated with TP concentrations (Fig. 3*a* for species richness; for the Simpson's diversity estimate, $r = -0.52$, $p = 0.02$). There was also a significant relationship when percent disturbance was used as a predictor variable for species richness (Fig. 3*b*) but not for Simpson's diversity estimates ($r = -0.36$, $p = 0.12$). Unlike many other studies (e.g., Dodson et al. 2000), we failed to detect a significant relationship between alpha diversity and lake area (Fig. 3*c* for species richness; for the Simpson's diversity estimate, $r = -0.34$, $p = 0.15$) or depth (for species richness, $r = 0.38$, $p = 0.10$; for the Simpson's diversity estimate, $r = 0.36$, $p = 0.12$). However, because we chose to focus on shallow lakes, the range of lake sizes was limited (1.8–77.8 ha and 0.56–10.9 m Z_{max}), and in turn, this may have precluded our ability to detect a significant effect of lake morphometry.

Historical and paleolimnological analyses

The first census division and subdivision land-use data for the Petit Lac Saint-François region were collected in 1871. At that time, the amount of land cleared for cropland and pastureland comprised 17% and 13% of the census division and subdivision, respectively. The spatial extent of these agricultural lands, however, peaked in the mid-1900s and then subsequently declined. The intensity of agriculture, measured by the change in the census division's net P load to watershed soils, peaked later (i.e., between 1971 and 1991). Most of the P inputs (on average, 80%) have come in the form of manure-derived P. Based on aerial photograph analyses, we know that the proportion of urban land at both the census division and census subdivision scale has always been very low (~5%; G.K. MacDonald, unpublished data).

Our ^{210}Pb data suggest that the sediment record covers the entire historical period (Fig. 4), and over this time period, the geochemical and biological analyses show strong changes, many of which are synchronous with land-use change. For example, the sedimentation rates to the lake have been accelerated since ~1950 (Fig. 4*b*). The sedimentary organic carbon content (measured as LOI 550) showed a strong decline between 1890 and 1940 in Petit Lac Saint-François and has remained relatively low since 1940 (Fig. 5). The magnetic susceptibility profile shows an opposite trajectory compared with the LOI 550 profile, with a trend towards increasing values between 1870 and 1950 and then values remaining high between 1950 and the present (Fig. 5). The fluxes of cladoceran remains, indicators of secondary production, increased markedly over the past ~20–30 years (Fig. 5). The changes in LOI 550 and magnetic susceptibility, as well as changes in the fluxes of *Bosmina* and chydorids, are all significantly correlated with one another ($r > |0.87|$, $p < 0.001$, $n > 14$). Similar to the surface sediments where the strongest predictor of cladoceran community composition was TP, we found that the strongest environmental predictor of *Bosmina* or chydorid flux was net P load to soils ($r = 0.93$ and 0.89, respectively, $p < 0.001$, $n = 14$). The sum of percent cropland and percent

Fig. 3. The relationship between rarefied chydorid species richness (*S*, 4.5–25.4 species, log-transformed) and (*a*) total phosphorus (TP, 0.9–154.5 μg·L^{-1}, log-transformed), (*b*) the proportion of disturbed watershed area (i.e., percent agricultural and urban lands (denoted as % dist), 0%–91.5%, arcsine square root (Arcsine sqrt) transformed), and (*c*) lake surface area (*A*, 1.8–77.8 ha, log-transformed) of the 20-lake EMAP surface sediment analysis.

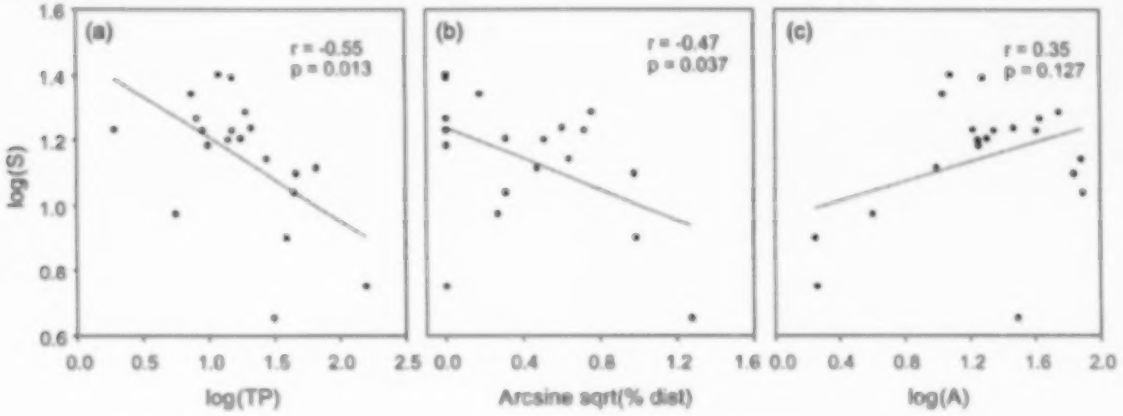
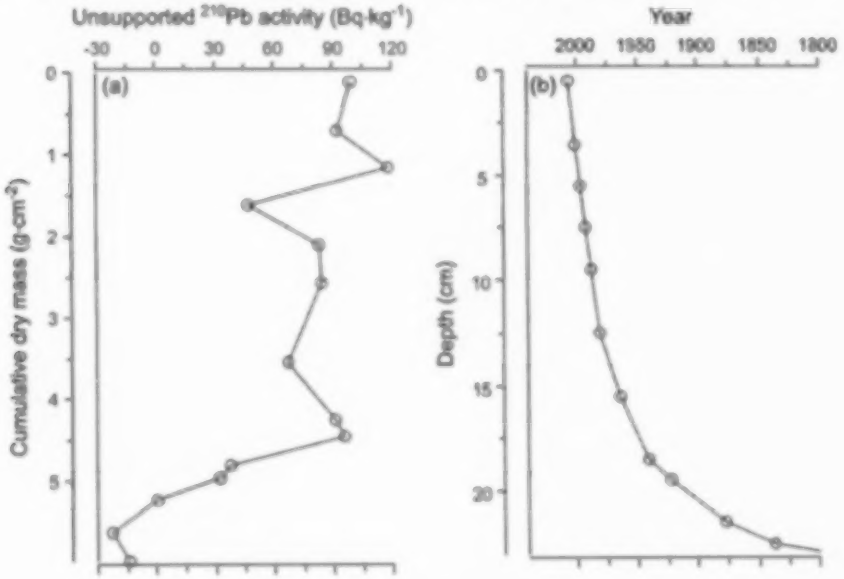


Fig. 4. (*a*) Changes in ^{210}Pb activity vs. sediment cumulative dry mass; (*b*) changes in sedimentation rate.



pastureland was not significantly related to either *Bosmina* or chydorid flux ($p > 0.05$).

The large changes in cladoceran fluxes were mirrored by pronounced shifts in cladoceran species composition and diversity. Specifically, *Alonella nana*, an oligotrophic indicator, showed a sharp decline in relative abundance in the early 1900s. Macrophyte-associated taxa also showed a decline towards the top of the core. These taxa are replaced by large expansions in the mesotrophic- and hypereutrophic-tolerant *Chydorus biovatus* and *Chydorus brevilabris* (Fig. 6). Plotting the cladoceran sediment core intervals passively in the RDA (which was developed based on modern cladoceran and environmental data) reveals that the Petit Lac Saint-François samples follow along the TP and pH vectors (Fig. 7).

The cladoceran assemblage shift also represents a major change in chydorid species richness. Rarefied species richness estimates show a significant decline from a maximum of 20.2 ± 1.6 species to a low of 10.5 ± 1.6 species at the surface, when comparing individual intervals (Fig. 6). The integrated-sample species richness and Simpson's index measures also show the same declining trend in species diversity (Fig. 6). Correlation analyses between the diversity metrics and net P load were all strongly negatively related ($r < -0.86$, $p < 0.001$, $n = 14$).

Discussion

Across spatial and temporal gradients, lake-water TP concentration and P load to watershed soils were significant

Fig. 5. Historical census division data and paleolimnological analyses from Petit Lac Saint-François. Human population densities represent measurements of number of people·km^{-2}. The sums of cropland and pastureland data are expressed as percentages of the entire census division, with the shaded area representing the percent area dedicated to cropland alone. The net P load to the watershed soils is the difference between P inputs (i.e., fertilizer P and P derived from livestock manure) and outputs (i.e., P removed in harvested crops), expressed as kg P·ha^{-1}·year^{-1}. LOI 550 is a measure of the percent organic content of the sediment. The units for magnetic susceptibility and fluxes of Cladocera groups are SI units·g^{-1} and individuals·cm^{-2}·year^{-1}, respectively. Because cladoceran flux and accumulation data (individuals·g dry weight^{-1}) were very similar, we have not shown the accumulation data (i.e., significant correlations were detected between flux and accumulation for each group of cladocerans). *Daphnia* remains may not preserve as well as other cladocerans, and thus we have focused our quantitative analyses on *Bosmina* and chydorids.

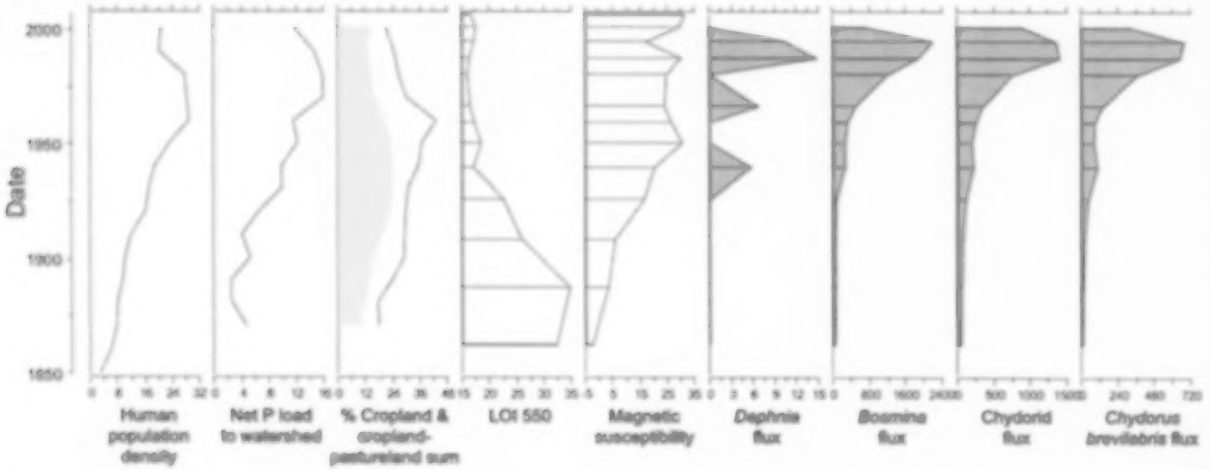
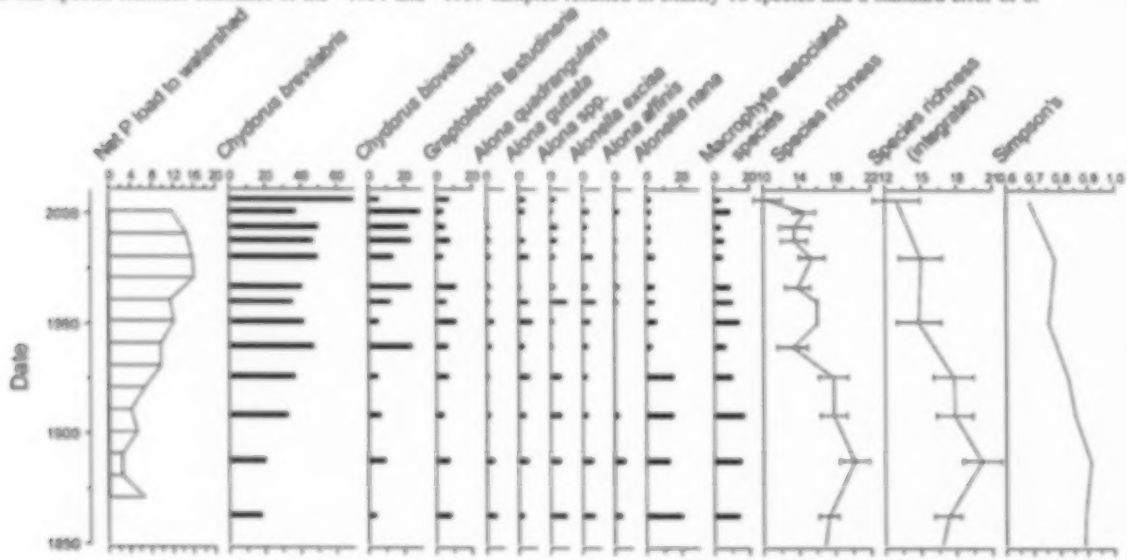
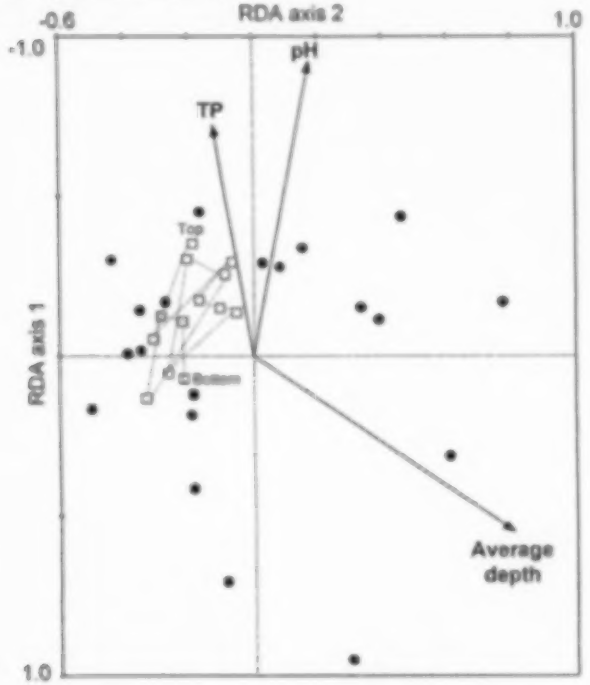


Fig. 6. Changes in the relative abundance (%) of chydorid species and diversity in the ~150-year sediment core record from Petit Lac Saint-François plotted alongside the net P load to the watershed. With the relative abundance data, only taxa that were present at greater than 5% abundance are shown. The taxa included in the macrophyte-associated cladoceran group are *Alona rustica*, *Alona intermedia*, *Pleuroxus* spp., *Eurycercus lamellatus*, and *Sida crystallina* (note that not all of these taxa are chydorids). Species richness was measured by individual-based rarefaction of raw chydorid counts ($n = 60$) for both individual and integrated sample assemblages to correct for changing sedimentation rate. Note that species richness estimates of the ~1951 and ~1959 samples resulted in exactly 16 species and a standard error of 0.



predictors of cladoceran community composition, diversity, and (or) secondary production (measured as changes in flux to the sediments). These results are consistent with previous ecological surveys and paleolimnological studies that have demonstrated significant relationships between phosphorus and Cladocera. Specifically, phosphorus is known to impact cladocerans directly as it is an essential nutrient and a component of several key biochemicals (Sterner and Hessen

Fig. 7. Redundancy analysis (RDA) of the EMAP surface sediment cladoceran assemblages (solid circles) with samples from Petit Lac Saint-François (open squares) plotted passively. The dotted lines connect sequential sediment intervals from the bottom (~1860) to the top of the core (2007).



1994). As such, phosphorus influences individual cladoceran growth when it is found in low concentrations in cladoceran food (i.e., algae; Urabe et al. 1997). Phosphorus also has an indirect influence on cladocerans, as it strongly controls the amount of algal growth. As has been found in many other studies (e.g., Prairie et al. 1989), we noted that TP is a significant predictor of chlorophyll *a* levels in the spatial survey, which in turn is a proxy for primary production (Dillon and Rigler 1974), an important food resource for herbivorous grazers such as cladocerans. TP may also affect the quality of prey for cladocerans by altering phytoplankton community composition, but this mechanism could not be addressed with the data available.

Pronounced ecological changes can occur in shallow lakes at elevated TP levels when phytoplankton biomass becomes so dense that it shades out submerged macrophytes (Scheffer et al. 1993, 2001). Submerged macrophytes are vital for certain littoral species (namely, *Alona rustica*, *Alona intermedia*, *Pleuroxus* spp., *Eurycercus lamellatus*, and *Sida crystallina*) that feed on epiphytes or require them as a substrate (Fryer 1968; Korhola and Rautio 2001). These taxa were predominantly found in mesotrophic waters in our spatial survey and were much less abundant in eutrophic waters, most likely due to the loss of macrophytes in nutrient-rich waters. In our sediment record of Petit Lac Saint-François, there is a discernable decrease in relative abundance of macrophyte-associated species that is broadly concurrent with the changes in net P load to the watershed soils. Based on our preliminary macrofossil analyses of this same core, there is also evidence to suggest that macrophytes were once very abundant in this lake (J.C. Vermaire, personal observation). Given that there are now very few macrophytes growing in Petit Lac Saint-François, we believe that the eutrophication of this lake resulted in a loss of macrophytes and associated epiphytic taxa.

Change in predation pressure is another important factor to consider when interpreting changes in Cladocera community structure (e.g., Jeppesen et al. 1996). Across our survey of lakes, it is likely that planktivorous predation pressure plays some role in shaping overall cladoceran community composition, but unfortunately, fish data were not available for our subset of EMAP lakes. In the Petit Lac Saint-François record, we suggest that chydorid composition is primarily reflecting changes in nutrients and macrophytes because these variables are stronger predictors of littoral community composition than fish predation (Jeppesen et al. 1996). Furthermore, the trajectory of our core data, within the context of the RDA derived from our spatial survey, suggests that the cladoceran assemblage, over time, shifted to one reflecting a more nutrient-rich community. Likewise, the consistent pattern evident across all flux profiles suggests that predation pressure is not the primary driver, as these groups differ in their sensitivity to planktivores.

Similar to previous work by Dodson et al. (2005, 2007), we detected a significant negative relationship between cladoceran diversity and the proportion of disturbed land in the watershed across lakes. This may be due, in part, to the dominance of eutrophic-tolerant taxa such as *Chydorus brevilabris* that are better able to compete at high nutrient levels or are not affected by toxic cyanobacteria and can exclude other species. A shift in the phytoplankton community towards larger, inedible filamentous primary producers, a phenomenon that can occur in more nutrient-rich waters (Kalff 2002), could also hamper the ability of some filter-feeding cladoceran taxa. Furthermore, eutrophication can lead to a decline or loss of macrophytes and their associated communities, which in turn, can decrease cladoceran diversity in nutrient-rich lakes.

In our temporal analysis, we found that land-use intensity rather than land cover was a significant predictor of chydorid diversity, as well as *Bosmina* and chydorid flux. Consistent with this finding, we note that previous paleolimnological studies have found that the clearing of vegetation from a watershed on its own may not result in a large or sustained change in lake-water P concentration (e.g., Räsänena et al. 2007). However, when land is cleared for agriculture and a sufficient amount of fertilizer is applied to watershed soils (either from animal manure or commercial fertilizer with applications that are in excess of crop requirements), the export of nutrients to surface waters is enhanced (Carpenter 2008). In our study, we found that increases in net P load to the watershed soils lagged behind increases in agricultural land cover. Net P load to regional soils, however, was correlated with both LOI 550 and magnetic susceptibility. The LOI 550 and magnetic susceptibility profiles reflect a progressive increase in minerogenic content of lake sediments, which is indicative of soil erosion (Boyle 2001; Sandgren and Snowball 2001). Given that LOI 550 is a relative measure, it would appear as though the increases in inorganic matter arising from the catchment outweigh any increased autochthonous organic matter production. The

strong correlations between LOI 550, magnetic susceptibility, or net P load to the watershed and cladoceran production or diversity imply that changes in the ecological functioning of Petit Lac Saint-François were driven by shifts in the intensity of agricultural activities rather than the spatial extent of agricultural land. We suggest that a spatial survey approach may be more apt to detect a strong interaction between biological indicators and the proportion of land use dedicated to agriculture, particularly in regions where land-use practices have not changed much in the past decade or more, because spatial surveys can provide a temporally integrated perspective of cumulative phosphorus loads.

Overall, our study has shown that changes in land use within the watershed, in particular those changes that result in increased phosphorus loading, can have a significant effect on the cladoceran community that ultimately results in the reduction of biodiversity. Our findings are consistent with those of Dodson et al. (2005, 2007) and demonstrate that watershed land use is a key structuring factor of cladoceran diversity and community composition. Our results also highlight that metrics of land-use intensity rather than cover may be more appropriate for defining the responses of aquatic ecosystems to land-use change.

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Appendix A

Table A1. Summary of ecological variables of the 20-lake EMAP data set.

Lake code	Lake name	Latitude (°N)	Longitude (°W)	Chlorophyll *a* ($\mu g \cdot L^{-1}$)	Conductivity ($\mu S \cdot cm^{-1}$)	Dissolved organic carbon ($mg \cdot L^{-1}$)	pH
CT002	Bissonette Pond	41.92	72.22	8.1	101	5.2	7.9
MA007	Upper Artichoke Reservoir	42.8	70.93	3.9	176	7.4	8.2
MA008	Savery Pond	41.91	70.84	11.1	81	5.6	7.3
ME001	Moose Pond	43.59	70.93	1.5	48	2.9	7.8
ME002	Mountain Pond	44.9	70.64	2.6	16	4.1	6.7
ME004	Shaw Pond	45.29	70.28	4.1	32	7.3	7.6
ME009	Alder Brook Stream	44.92	69.25	3.5	124	7.5	8.4
ME011	Female Pond	45.75	69.22	3.4	32	6.9	7.6
NH006	Flints Pond	42.75	71.55	4.1	143	6.4	8.2
NH009	Russell	44.01	71.65	2.0	21	1.9	6.8
NJ002	Cranberry Lake	40.95	74.75	22.8	142	5.1	8.2
NY021	Gerlach Pond	42.32	78.98	34.9	87	6.2	8.1
NY023	Crystal Lake	43.83	76.13	15.1	236	4.2	8.5
NY024	White Lake	43.01	76.04	1.2	1073	2.1	8.5
NY025	Hyde Lake	44.24	75.83	26.8	122	3.4	8.1
NY032	Windfall Pond	44.36	74.45	4.8	24	3.6	7.3
NY036	Masich's Pond	42.63	74.32	6.0	136	4.7	8.4
RI004	Mashapoag	41.79	71.43	21.4	345	5.2	8.3
VT005	Ticklenaked	44.19	72.1	6.3	180	4.3	8.4
VT009	Abanaki	43.83	72.23	4.2	72	4.7	8.1

Note: NTU, nephelometric turbidity units.

Appendix B

Table B1. List of all identified Cladocera species.

EMAP data set species list	PSF core species list
Acroperus harpae	*Acroperus harpae*
Alona affinis	*Alona affinis*
Alona barbabulata	*Alona circumfibriata*
Alona bicolor	*Alona costata*
Alona circumfibriata	*Alona guttata*
Alona costata	*Alona intermedia*
Alona guttata	*Alona quadrangularis*
Alona intermedia	*Alona rustica*
Alona quadrangularis	*Alona* spp.
Alona rustica	*Alonella dentifera*
Alona setulosa	*Alonella excisa*
Alona spp.	*Alonella exigua*
Alonella dentifera	*Alonella nana*
Alonella excisa	*Bosmina longirostris*
Alonella exigua	*Bosmina longispina*
Alonella nana	*Camptocercus* spp.
Bosmina longirostris	*Chydorus biovatus*
Bosmina longispina	*Chydorus brevilabris*
Camptocercus spp.	*Chydorus faviformis*
Chydorus bicornutus	*Chydorus gibbus*
Chydorus biovatus	*Chydorus piger*
Chydorus brevilabris	*Daphnia pulex*
Chydorus faviformis	*Daphnia* spp.
Chydorus gibbus	*Disparalona leei*
Chydorus piger	*Eurycercus lamellatus*
Daphnia longispina	*Graptoleberis testudinaria*
Daphnia pulex	*Kurzia latissima*
Daphnia spp.	*Latona setifera*
Diaphanosoma brachyurum	*Leydigia leydigii*
Disparalona acutirostris	*Monospilus dispar*
Disparalona rostrata	*Pleuroxus aduncus*
Dunhevedia crassa	*Pleuroxus denticulatus*
Eurycercus lamellatus	*Pleuroxus laevis*
Graptoleberis testudinaria	*Pleuroxus procurvus*
Kurzia latissima	*Pleuroxus* spp.
Latona setifera	*Pleuroxus striatus*
Leptodora kindti	*Pleuroxus trigonellus*
Leydigia leydigii	*Pleuroxus truncatus*
Monospilus dispar	*Pleuroxus uncinatus*
Oxyurella tenuicaudis	*Sida crystallina*
Pleuroxus aduncus	
Pleuroxus denticulatus	
Pleuroxus laevis	
Pleuroxus procurvus	
Pleuroxus spp.	
Pleuroxus trigonellus	
Pleuroxus truncatus	
Pleuroxus uncinatus	
Pseudochydorus globosus	
Rhynchotalona falcata	
Sida crystallina	

Total nitrogen ($\mu g \cdot L^{-1}$)	Total phosphorus ($\mu g \cdot L^{-1}$)	Turbidity (NTU)	Mean depth (m)	Lake surface area (ha)	Agriculture in watershed (%)	Disturbance in watershed (%)	Estimated watershed slope (%/100)
400	16.5	1.3	1.3	20.1	3.1	9.2	0.04
500	18.0	1.0	1.4	55.3	44.9	47.0	0.02
550	64.3	9.4	1.4	9.8	18.2	20.5	0.01
300	6.4	0.4	2.6	10.7	0.0	3.1	0.03
300	10.9	0.7	3.8	11.9	0.0	0.0	0.14
400	14.0	0.9	1.2	18.9	0.0	0.0	0.06
500	20.0	1.4	0.8	29.3	30.6	32.0	0.01
300	7.9	0.7	8.4	40.2	0.0	0.0	0.06
470	13.0	1.9	1.3	17.5	20.0	23.5	0.03
300	0.9	0.2	10.9	16.4	0.0	0.0	0.16
600	43.5	3.0	1.9	77.8	0.0	9.4	0.04
900	154.5	7.8	0.6	1.8	0.0	0.0	0.10
600	45.0	1.4	3.1	68.1	68.5	68.5	0.01
1060	4.6	0.2	5.5	4.0	0.0	7.0	0.08
500	26.5	2.8	3.4	75.9	34.0	35.4	0.01
300	7.0	0.7	3.0	42.3	0.0	0.0	0.07
500	37.9	1.4	2.1	1.8	69.6	69.6	0.15
800	30.0	6.8	1.9	30.8	0.0	91.5	0.01
400	14.0	2.1	7.2	22.2	42.1	43.2	0.04
400	8.8	0.5	1.6	17.7	0.0	0.0	0.08

A comparison of stock and individual identification for sockeye salmon (*Oncorhynchus nerka*) in British Columbia provided by microsatellites and single nucleotide polymorphisms

Terry D. Beacham, B. McIntosh, and C. Wallace

Abstract: Variation at 14 microsatellite loci, one major histocompatibility complex (MHC) locus, and 49 single nucleotide polymorphism (SNPs) loci was surveyed in 44 populations of sockeye salmon (*Oncorhynchus nerka*) over 16 regions from southern and central British Columbia, Canada. Sequential addition of the five highest rated SNPs to the suite of 14 microsatellites provided the equivalent average accuracy when compared with the current suite of microsatellites and MHC. Six microsatellites provided the equivalent average stock identification resolution and individual assignment accuracy compared with 46 SNPs. For regional stock compositions, 53–104 SNPs were projected to be required to provide accuracy and precision equivalent to the microsatellites. For population-specific stock compositions, 75–79 SNPs were projected to be required to provide accuracy and precision equivalent to the microsatellites. Equivalency in individual assignment accuracy to region was estimated to require 100 SNPs of the quality evaluated in the study, whereas equivalent accuracy in assignment to specific populations was estimated to require 124 SNPs. Applications that incorporate the existing power of a combined microsatellite–SNP approach are the best current technique available for sockeye salmon stock identification applications in southern British Columbia.

Résumé : Nous avons inventorié la variation à 14 locus microsatellites, un locus d'un complexe majeur d'histocompatibilité (MHC) et 49 locus de polymorphismes mononucléotidiques (SNP) dans 44 populations de saumons rouges (*Oncorhynchus nerka*) réparties dans 16 régions du sud et du centre de la Colombie-Britannique, Canada. L'addition séquentielle des cinq SNP ayant la plus forte cote à la suite des 14 microsatellites procure une exactitude moyenne équivalente à celle de la suite courante des microsatellites et du MHC. Six microsatellites fournissent une résolution moyenne d'identification des stocks et une exactitude des assignations individuelles équivalentes à 46 SNP. Pour ce qui est de la composition régionale des stocks, nous extrapolons qu'il faudrait 53–104 SNP pour obtenir une exactitude et une précision équivalentes à celles des microsatellites. Dans le cas des compositions de stocks spécifiques aux populations, 75–79 SNP seraient nécessaires pour obtenir l'exactitude et la précision équivalentes à celles des microsatellites. Nous estimons que, pour obtenir une équivalence dans l'exactitude des assignations individuelles à la région, il faudrait 100 SNP de même qualité que ceux évalués dans notre étude; pour une exactitude équivalente dans l'assignation à une population spécifique, il faudrait 124 SNP. Les applications qui incorporent la puissance connue de l'utilisation combinée des microsatellites et des SNP constituent la meilleure méthodologie couramment disponible pour l'identification des stocks de saumons rouges dans le sud de la Colombie-Britannique.

[Traduit par la Rédaction]

Introduction

Management of salmon fisheries targeting Fraser River sockeye salmon (*Oncorhynchus nerka*) in southern British Columbia and Washington is reviewed and directed by the Fraser River Panel of the Pacific Salmon Commission (PSC), with the Panel composed of fishers, managers, and assessment staff of both Canada and the United States. There are two main sources of information required in the determination of weekly management decisions, namely the abundance of sockeye salmon that is present and the stock composition of that abundance (Woodey 1987). Genetic stock identification (GSI) is an important part of the management process, and results are used to assess stock-

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specific timing and abundance patterns. Daily and weekly estimates of sockeye salmon abundance and stock composition from test fisheries are used to manage fisheries so that harvest and escapement goals can be achieved. Prior to 2009, GSI of sockeye salmon in fisheries in this region was conducted with a set of 14 microsatellites and one major histocompatibility complex (MHC) locus (Beacham et al. 2004*a*), with accuracy of estimates confirmed by a number of blind sample tests (Beacham et al. 2004*b*). Management of Fraser River sockeye salmon requires that stock composition estimates be available within an 8 to 24 h period after sample arrival in the laboratory (Beacham et al. 2004*a*). Estimates of stock composition derived solely from microsatellites are available within an 8 h period, but incorporation of MHC variation requires a 24 h analysis. Rapid estimates of stock composition are required for incorporation into in-season management decisions, with estimates of stock composition based only on microsatellites sometimes used in decisions, with subsequent incorporation of MHC variation into the estimates the following day generally confirming decisions reached the previous day. Final estimates of stock composition available the same day as sample delivery would be beneficial. Incorporation of markers for Fraser River sockeye salmon GSI applications require stock composition estimates to the individual population or tributary in many cases, as well as identification of individuals to specific populations or tributaries (Cooke et al. 2006; Young et al. 2006; Macdonald et al. 2009).

Although application of the 14 microsatellites and the MHC locus meet current resolution and cost requirements, there may be other stock identification techniques available that may provide advantages of increased resolution at lower cost per individual. The most widely promoted current technique is the application of single nucleotide polymorphisms (SNPs). The benefits of applying SNPs relative to microsatellites were suggested to be ease of data standardization among laboratories, high throughput, high diversity among populations, low genotyping errors, and low cost of analysis per individual (Smith et al. 2005*a*, 2005*b*). Indeed, a panel convened to evaluate the coded wire tagging program in Pacific salmon recommended that "the Pacific Salmon Commission support an immediate evaluation of the coordinated transition for all salmon species from genetic stock identification (GSI) based on the use of microsatellite markers to GSI based on single nucleotide polymorphism (SNP) markers" (PSC 2005, p. 32). As a functioning GSI program for sockeye salmon in Washington and British Columbia based on microsatellites and MHC variation predated this report (Beacham et al. 2004*a*, 2004*b*), but SNP variation had not been investigated for Washington or British Columbia sockeye salmon, it was not possible to conduct an immediate evaluation of a proposed transition for GSI applications from microsatellites to SNPs. Accordingly, there was no scientific consensus as to the preferred approach to apply in GSI of Pacific salmon. Subsequently, a report derived from two GSI-based workshops recommended that "the PSC should continue to support microsatellites as a demonstrated coast-wide tool for GSI for Chinook salmon and continue to support the development of SNPs. Both microsatellites and SNPs have demonstrated capabilities in estimation of stock composition. The value of SNPs has been clearly demonstrated at a regional level, but the effectiveness of a coast-wide application of SNPs remains to be explored" (PSC 2008, p. 10). The report noted that "Additional comparisons of current and future costs and performance of microsatellites and SNPs will be required before an objective selection of a single approach might be justified" (PSC 2008, p. 11).

SNPs are currently applied to estimate stock compositions of sockeye salmon fisheries in Alaska. A suite of 45 SNPs has been used to estimate stock compositions of sockeye salmon in Cook Inlet fisheries (Habicht et al. 2007), and the authors indicate that this same suite of SNPs has been used in GSI applications for management of Bristol Bay sockeye salmon, as well as in the Northern Boundary area (area adjacent to the international border) in Southeast Alaska. In the Northern Boundary area, fisheries intercept sockeye salmon bound for both Southeast Alaskan and Canadian rivers, and managers and assessment staff from both the United States (US) and Canada need to be satisfied that reliable estimates of stock composition are provided by GSI applications. The 14 microsatellites and MHC locus have been previously tested and demonstrated to provide high resolution in stock composition estimates for fisheries in the area (Beacham et al. 2005*a*), and this is the technology applied in GSI of Northern Boundary sockeye salmon fisheries on the Canadian side of the border. SNPs are applied on the US side of the border (in addition to scale pattern analysis), but a definitive test of stock identification resolution provided by SNPs has yet to be conducted.

Before conclusions can be drawn on the efficacy of microsatellites and SNPs for sockeye salmon GSI applications, comparisons between the two techniques obviously must be conducted. The focus of any evaluation would be the resolution of stock composition estimates provided by the two techniques and the cost per individual required to obtain the observed resolution. The key question to answer is how many SNPs must be used to provide stock composition estimates of equivalent quality in terms of both accuracy and precision when compared with estimates produced with an existing microsatellite baseline. Alternatively, if the resolution required for existing management applications is satisfactorily determined from a suite of SNPS, how many microsatellites must be analyzed to provide comparable resolution of stock composition in terms of accuracy, precision, and individual assignment. Initial comparisons of the efficacy of microsatellites and SNPs for stock and individual identification of Chinook salmon (*Oncorhynchus tshawytscha*) were reported by Beacham et al. (2008) and Narum et al. (2008), but no comparison has been conducted for sockeye salmon.

In the current study, we evaluate the utility of using variation at 14 microsatellite loci and a MHC locus for stock identification applications for 44 populations of sockeye salmon ranging from the central coast of British Columbia to the Fraser River, with emphasis on Fraser River populations. We also evaluate the accuracy and precision of estimates of stock composition derived from a suite of 49 SNPs (the 45 SNPs outlined by Habicht et al. (2007) plus four SNPs identified in our laboratory) from the same 44-population baseline. The following key questions were investigated. (*i*) How many SNPs are required to replace the MHC locus in GSI applications for Fraser River sockeye salmon with no

loss of average population resolution? (*ii*) How many microsatellites are required to provide equivalent stock identification resolution to that of the 49 SNPs? (*iii*) How many SNPs are required to replace the current 14 microsatellite baseline used in GSI applications?

Materials and methods

Collection of DNA samples and laboratory analysis

Tissue samples were collected from mature sockeye salmon from 44 populations ranging from the central coast of British Columbia to the Fraser River drainage, with the majority of the populations surveyed from the Fraser River (Table 1; Fig. 1). Samples were generally preserved in 95% ethanol and sent to the Molecular Genetics Laboratory at the Pacific Biological Station (Nanaimo, British Columbia). Historical scale samples were accessed occasionally as well. DNA was extracted from the tissue or scale samples using a variety of methods, including a chelex resin protocol outlined by Small et al. (1998), a Qiagen 96-well Dneasy® procedure, or a Promega Wizard SV96 Genomic DNA purification system. Once extracted DNA was available, variation at microsatellite, MHC, and SNP loci was surveyed. For the microsatellites, polymerase chain reaction (PCR) products at 14 microsatellite loci (*Ots2*, *Ots3* (Banks et al. 1999); *Ots100*, *Ots103*, *Ots107*, and *Ots108* (Beacham et al. 1998; Nelson and Beacham 1999); *Oki1* (two loci), *Oki6*, *Oki10*, *Oki16*, and *Oki29* (Smith et al. 1998); *One8* (Scribner et al. 1996), and *Omy77* (Morris et al. 1996)) were initially size-fractionated in denaturing polyacrylamide gels using an ABI 377 automated DNA sequencer, and genotypes were scored by Genotyper 2.5 (Applied Biosystems, Foster City, California) using an internal lane sizing standard. Later in the study, microsatellites were size-fractionated in an ABI 3730 capillary DNA sequencer, and genotypes were scored by GeneMapper 3.0 (Applied Biosystems, Foster City, California) using an internal lane sizing standard. Allele scores derived from Genotyper or GeneMapper were verified by either one or two laboratory personnel. Repeatability of genotyping was evaluated by repeat PCR analysis and scoring of approximately 500 fish. Discrepancies in scoring were observed in 21 genotypes of 6720 genotypes scored across all loci, for a genotyping error rate of 0.31%. Allele identification between the two sequencers were standardized by analyzing approximately 600 individuals on both platforms and converting the sizing in the gel-based data set to match that obtained from the capillary-based set.

Genetic variation at the MHC class II *DAB*-β1 locus (Miller et al. 2001) was surveyed by denaturing gradient gel electrophoresis (DGGE). β1 alleles were separated by DGGE with the Bio-Rad (Hercules, California) D Gene™ or D Code™ electrophoresis systems, with conditions determined by the methods of Miller et al. (1999). Fluorescently multiplexed (FM) DGGE (Miller et al. 2000) was used in the population survey, with scoring of genotypes conducted by one individual.

Variation was analyzed at 49 SNPS (46 nuclear, three mitochondrial), with the 45 SNPs outlined by Habicht et al. (2007) supplemented by an additional four SNPs. SNPs added by our laboratory were as follows: *One-Hsp47* primer sequences F: CGT TCA AAT AAA TGC TGT TTG GCC TTT, R: GTG GTG TTC GGA TTT TTC CTG AAA; probe sequences: VIC-TTA TTG ACT ATG GCA CAT TG, FAM-TTG ACT ATG GCG CAT TG; *One-PIP1* primer sequences F: ACA GAG TCA GGA CTT GAT ATG TAC AGA, R: CCT GAC GAG GGT CTA CTA CAC T, probe sequences: VIC-AAC ACA CAT TTC TCA ACA CA, FAM-ACA CAC ATT TTT CAA CAC A; *One-SEPP* primer sequences F: GGA TGG AGG GAG CAA AAC AGA, R: ACC CTC CCA GGA GTG TAT GG, probe sequences: VIC-AAA CGT TAA CAT AAT CAC C, FAM-AAA CGT TAA AAT AAT CAC C; and *One-C1259* primer sequences F: GCA TTT CTC AAC CCC ACA ACA C, R: CCT ATT TAG GGC TCT ATT TCT GTG AG, probe sequences: VIC-ACT GGG AAC TAT TTA AAA, FAM-CTG GGA ACT ATT AAA AA. The listing of all SNPs surveyed is outlined in Table 2. After PCR amplification, the plates (384 wells) were read on an ABI Prism 7900HT sequence detection system by one individual using sequence detection software from ABI. Repeatability of genotyping was evaluated by repeat PCR analysis and scoring of genotypes in approximately 190 fish, with discrepancies in scoring observed in 21 genotypes of 5320 genotypes scored across all loci, for a genotyping error rate of 0.39%.

Estimation of stock composition in single-population samples

Two software packages were utilized in estimation of stock composition of single-population mixtures: Statistical Package for the Analysis of Mixtures (SPAM, version 3.7) (Debevec et al. 2000) and ONCOR (Kalinowski et al. 2007). Three mitochondrial (mt) DNA SNPs were analyzed in the survey, and as ONCOR is currently unable to analyze variation incorporating mitochondrial haplotypes, SPAM was used exclusively for those analyses incorporating mitochondrial SNPs. Genotypic frequencies were determined for each locus in each population and were used to estimate stock composition of simulated single-population samples. The Rannala and Mountain (1997) correction to baseline allele frequencies was used for SPAM analyses to avoid the occurrence of fish in the mixed sample from a specific population having an allele not observed in the baseline samples from that population. All diploid loci were considered to be in Hardy–Weinberg equilibrium (microsatellites (Beacham et al. (2006*a*), SNPs (T.D. Beacham, B. McIntosh, and C. Wallace, unpublished data)), and expected genotypic frequencies were determined from the observed allele frequencies. Reported stock compositions for simulated single-population samples are the bootstrap mean estimate of each mixture of 200 fish analyzed, with mean and variance estimates derived from 100 bootstrap simulations. Each baseline population and simulated single-population sample was sampled with replacement to simulate random variation involved in the collection of the baseline and fishery samples. When ONCOR was used to estimate stock compositions, the Rannala and Mountain (1997) correction to baseline allele frequencies was again implemented, with precision of the stock composition estimates calculated by bootstrapping over observed baseline population sample sizes and a mixture size of 200 fish. For both SPAM and ONCOR, allocations to individual baseline populations were summed to provide estimates of stock compositions for regional stock

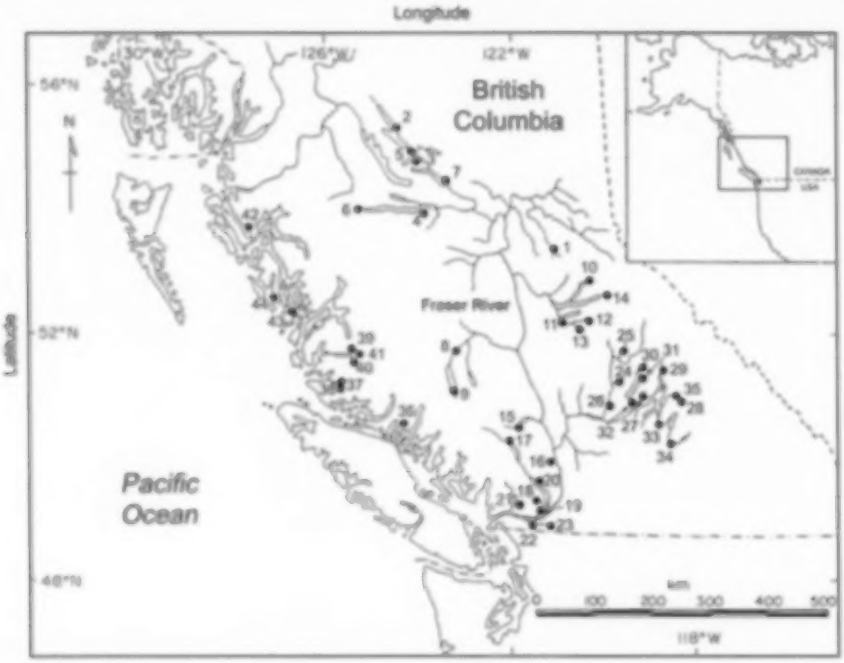
Table 1. Regions, populations surveyed within regions, realized sample sizes per locus for SNPs, MHC, and microsatellites (Micros) for 44 populations of sockeye salmon from 16 regions in British Columbia, as well as stock composition for single-population samples estimated for a suite of 14 microsatellites plus MHC and a suite of 14 microsatellites plus the five highest-rated SNPs, with stock composition estimated using two software packages (SPAM and ONCOR).

		Sample size			SPAM		ONCOR	
Region	Population	SNPs	MHC	Micros	Micros + MHC	Micros + 5 SNPs	Micros + MHC	Micros + 5 SNPs
Upper Fraser	(1) Bowron Lake	85.5	200	217.1	97.82	97.68	99.79	99.56
Early Stuart	(2) Takla Lake	185.6	140	283.4	81.94	81.95	64.69	65.79
Early Stuart	(3) Trembleur Lake	370.1	346	490.8	90.73	91.52	79.47	80.58
Stuart–Nechako	(4) Stellako River	92.5	414	312.6	96.52	96.44	96.78	97.00
Stuart–Nechako	(5) Middle River	84.7	344	282.4	95.50	95.18	93.12	93.62
Stuart–Nechako	(6) Nadina River	93.5	328	329.6	97.36	97.41	98.86	98.99
Stuart–Nechako	(7) Pinchi Creek	93.0	105	85.1	76.52	78.38	58.63	60.27
Chilko	(8) Chilko River	89.9	597	480.9	96.42	96.08	94.57	94.63
Chilko	(9) Chilko Lake south	92.9	330	334.8	94.43	94.75	90.08	89.90
Quesnel	(10) Mitchell River	72.6	244	208.1	94.92	95.14	93.35	93.39
Quesnel	(11) Lower Horsefly	78.5	171	192.1	77.14	76.78	51.85	50.18
Quesnel	(12) Upper Horsefly	84.9	386	420.1	89.61	87.25	71.20	68.28
Quesnel	(13) McKinley Creek	86.1	177	192.9	69.36	72.02	37.65	42.35
Quesnel	(14) Blue Lead Creek	87.3	91	89.7	87.32	87.02	75.87	78.20
Canyon	(15) Gates Creek	79.3	321	341.8	98.88	98.91	99.96	99.96
Canyon	(16) Nahatlatch River	94.1	214	217.3	98.12	98.04	99.91	99.84
Harrison	(17) Birkenhead River	71.3	323	261.8	98.20	98.29	99.52	99.60
Harrison	(18) Weaver Creek	78.7	462	443.7	98.69	98.76	99.69	99.76
Harrison	(19) Harrison River	77.3	230	240.2	97.71	97.56	99.36	99.35
Harrison	(20) Big Silver Creek	92.6	155	182.4	97.45	97.53	99.68	99.60
Lower Fraser	(21) Pitt Lake	90.0	326	378.8	98.91	98.91	99.71	99.74
Chilliwack	(22) Cultus Lake	93.7	785	1687.1	99.84	99.76	100.00	100.00
Chilliwack	(23) Chilliwack Lake	93.3	156	206.9	98.29	98.10	99.96	99.96
North Thompson	(24) Fennell Creek	91.7	391	424.0	97.79	97.69	98.29	98.25
North Thompson	(25) Raft River	88.2	264	269.6	94.68	94.70	93.68	93.23
North Thompson	(26) North Thompson	93.5	144	177.9	92.94	93.06	90.86	90.88
Shuswap Early	(27) Scotch Creek	90.5	245	343.3	94.72	94.63	92.08	90.96
Shuswap Early	(28) Eagle River (early)	88.8	154	183.4	94.40	94.63	94.57	94.53
Shuswap Early	(29) Seymour Creek	92.8	166	224.6	91.03	90.58	86.06	86.00
Shuswap Early	(30) Upper Adams River	83.9	329	353.3	97.98	98.24	99.17	99.32
Shuswap Early	(31) Cayenne Creek	88.7	87	87.1	89.09	89.65	94.96	94.81
Shuswap Late	(32) Lower Adams River	83.6	310	251.9	92.39	91.42	85.24	84.57
Shuswap Late	(33) Lower Shuswap	92.0	217	192.9	85.33	86.03	64.87	64.81
Shuswap Late	(34) Middle Shuswap	87.7	200	226.9	88.66	88.41	76.23	76.30
Shuswap Late	(35) Eagle River (late)	87.4	72	161.4	86.16	84.89	70.73	70.47
South Coast	(36) Phillips River	90.6	163	176.1	98.30	98.35	99.91	99.89
Long Lake	(37) Smokehouse Creek	86.7	138	127.6	86.60	86.01	64.17	63.94
Long Lake	(38) Canoe Creek	85.9	127	129.0	88.82	88.91	63.72	63.39
Owikeno	(39) Washwash River	93.2	264	316.4	87.11	87.38	71.96	74.42
Owikeno	(40) Neechanz River	93.3	288	307.9	87.34	86.56	65.35	64.02
Owikeno	(41) Sheemahant River	92.8	270	277.3	84.30	83.38	60.01	61.44
Central Coast	(42) Devon Lake	88.4	119	279.8	98.85	98.81	99.95	99.95
Central Coast	(43) Tankeeah River	94.4	301	377.1	99.25	99.22	99.97	99.97
Central Coast	(44) Kent Lake	87.2	88	94.1	96.47	96.59	99.95	99.97
Mean		96.5	254.2	292.3	92.36	92.33	85.81	85.95

groups (Table 1). Additionally, ONCOR was used to provide estimates of accuracy of identification of individuals to specific populations or regional stock groups.

The effect of population sample size on average accuracy of estimated stock compositions for both population-specific and regional estimates, as well as individual assignment accuracy to population and region, was investigated for SNPs with ONCOR for population sample sizes ranging from 20, 40, 60, 80, and 95 individuals, with samples of the appropriate size created by sampling existing population samples

Fig. 1. Map indicating locations of 44 sockeye salmon populations surveyed in British Columbia, Canada. Population names are provided in Table 1.



without replacement. Mean accuracy for each population sample size was determined as the average estimate across all 44 populations.

Relative ranking of the loci

The power of individual loci for stock composition estimation was initially evaluated by incorporating only a single locus for estimation of stock composition of single-population samples. As mtSNPs were included in the analysis, only SPAM was used to provide estimates of stock composition for all 44 single-population samples. Mean accuracy was determined as the average estimate across all 44 populations, with loci then ordered from the most accurate to the least accurate (Table 2). Weir and Cockerham's (1984) F_{ST} estimates for each locus over all populations were calculated with FSTAT (version 2.9.3.2; Goudet 1995). Allele frequencies for all populations surveyed in this study are available at the Molecular Genetics Laboratory Web site at www-sci.pac.dfo-mpo.gc.ca/mgl/default_e.htm.

How many SNPs for MHC equivalency?

SPAM and ONCOR were used to assess the number of SNPs that would be required to be analyzed to maintain the stock identification resolution provided by the MHC locus. The 14 microsatellites and the MHC locus were used to estimate stock composition of 44 single-population samples as described previously. Accuracy and standard deviation were then averaged over the 44 single-population simulations to provide the baseline case. Next, individual SNPs (starting with the locus with highest mean population accuracy) were added to the suite of 14 microsatellites, and average resolution of stock compositions was determined. Additional SNPs were then added until the average population accuracy and precision of stock composition estimates provided by the suite of microsatellites and SNPs matched that provided by the microsatellites and MHC locus.

How many microsatellites for SNP equivalency?

ONCOR was used exclusively for this analysis, with the proviso that the three SNPs of mtDNA origin were eliminated from the analysis, as they provided little power for GSI applications. The microsatellite locus with the highest average population accuracy was initially incorporated into the analysis, and lower accuracy microsatellites were sequentially added to the analysis until the average population accuracy and precision of stock composition estimates provided by the suite of microsatellites matched that provided by the 46 SNPs. Single-population samples were analyzed with the best 3, 4, 5, 6, 8, 10, 12, and 14 microsatellites. Accuracy and standard deviation for population- and region-specific estimates of stock composition were determined and were then averaged over the 44 single-population simulations for each set of loci. Percentage of individuals correctly assigned to specific populations and regions was also determined for all 44 populations, which was then averaged over all populations for each set of microsatellites evaluated.

How many SNPs for microsatellite equivalency?

Projections of the number of number of SNPs required for equivalency of the current microsatellite baseline were conducted by ranking SNPs according to the average accuracy observed in estimation of stock composition for single-population samples over the 44 populations surveyed. The mtDNA SNPs were eliminated in the analyses.

Table 2. Ranking of 64 markers for average estimated composition (population and regional accuracy determined with SPAM) of single-population samples over 44 populations of sockeye salmon, as well as F_{ST} values.

		Population, %		Region, %		
Marker	Type	Mean	SD	Mean	SD	F_{ST}
(1) *Ots100*	M	81.2	10.6	90.1	6.2	0.130
(2) *Oki16*	M	80.8	12.1	89.3	7.4	0.125
(3) *Oki29*	M	79.0	9.6	87.5	6.3	0.075
(4) *Ots108*	M	78.3	10.4	87.6	6.5	0.061
(5) *Oki10*	M	77.1	9.6	83.7	7.4	0.028
(6) *Ots103*	M	76.3	10.8	83.3	8.1	0.057
(7) *Omy77*	M	73.3	13.1	81.7	9.5	0.103
(8) *Ots2*	M	73.3	13.3	84.0	8.5	0.108
(9) *Oki6*	M	71.7	16.2	80.7	11.8	0.141
(10) *One8*	M	68.7	15.7	78.4	12.3	0.082
(11) *Beta-1*	MHC	68.4	18.7	82.0	12.4	0.245
(12) *Ots3*	M	66.2	18.9	77.0	13.9	0.068
(13) *Ots107*	M	54.8	22.3	68.1	19.0	0.087
(14) *Oki1a*	M	43.6	24.0	57.9	22.7	0.085
(15) *Oki1b*	M	34.6	23.6	45.4	22.6	0.045
(16) *One-MHC2–190*	S	16.0	11.6	27.7	14.7	0.309
(17) *One-MHC2–251*	S	15.4	11.1	27.1	13.2	0.330
(18) *One-HPAL-99*	S	15.1	9.5	25.0	11.3	0.200
(19) *One-GPH-414*	S	15.0	9.6	25.3	10.5	0.218
(20) *One-U503–170*	S	13.4	10.6	26.1	12.2	0.207
(21) *One-RAG3–93*	S	13.4	9.2	25.1	10.4	0.141
(22) *One-ZP3B-52*	S	13.1	8.9	20.7	10.9	0.121
(23) *One-ACBP-79*	S	12.6	8.4	21.7	10.0	0.091
(24) *One-TF-EX3–182*	S	12.2	10.2	21.5	12.5	0.182
(25) *One-RF-112*	S	12.1	7.8	20.3	10.2	0.145
(26) *One-STR07–190*	S	11.8	9.6	22.4	12.6	0.178
(27) *One-HGFA-100*	S	11.7	8.5	21.0	11.3	0.105
(28) *One-HCS71–220*	S	11.6	8.1	22.2	11.8	0.129
(29) *One-U401–224*	S	11.5	6.2	19.3	8.5	0.065
(30) *One-C1259*	S	11.4	8.5	19.3	11.1	0.092
(31) *One-LEI-87*	S	11.1	6.7	19.1	8.4	0.057
(32) *One-TF-EX10–750*	S	11.0	7.02	19.5	9.6	0.074
(33) *One-STC-410*	S	10.9	8.9	22.6	9.2	0.254
(34) *One-GPDH-360*	S	10.4	8.8	20.4	11.2	0.111
(35) *One-ALDOB-135*	S	10.4	7.0	20.9	9.6	0.078
(36) *One-SEPP*	S	10.4	7.5	22.6	8.8	0.064
(37) *One-U404–229*	S	10.3	9.0	21.3	10.5	0.114
(38) *One-GPDH2–211*	S	10.0	9.2	19.3	11.5	0.140
(39) *One-PLNS-107*	S	9.9	6.3	15.3	8.1	0.051
(40) *One-U508–533*	S	9.9	8.1	21.0	11.6	0.063
(41) *One-OTS213–181*	S	9.8	8.5	18.9	10.2	0.107
(42) *One-HSP47*	S	9.7	8.0	18.6	10.5	0.082
(43) *One-U301–92*	S	9.7	8.5	20.4	9.2	0.093
(44) *One-VIM-569*	S	9.6	7.4	14.8	8.8	0.063
(45) *One-HPAL-436*	S	9.5	6.9	18.5	9.8	0.066
(46) *One-PIP-1-PIP3*	S	9.3	7.0	16.5	9.5	0.059
(47) *One-P53–576*	S	9.3	7.0	16.3	8.8	0.085
(48) *One-RAG1–103*	S	9.2	7.1	16.3	8.8	0.079
(49) *One-U504–141*	S	9.0	9.1	21.9	11.9	0.085
(50) *One-PRL2*	S	9.0	7.7	16.2	10.1	0.053
(51) *One-CTGF-301*	S	8.9	7.3	18.5	11.1	0.067
(52) *One-ZNF-61*	S	8.7	6.9	15.8	9.7	0.053
(53) *One-SERPIN-104*	S	8.6	8.5	17.7	10.7	0.157
(54) *One-IL8R-362*	S	8.6	6.9	15.1	8.8	0.061

Table 2 (*concluded*).

Marker	Type	Population, %		Region, %		F_{ST}
		Mean	SD	Mean	SD	
(55) *One-RF-295*	S	8.6	6.0	15.7	8.5	0.087
(56) *One-GHII-2461*	S	8.6	7.9	14.4	9.8	0.046
(57) *One-RH2OP-395*	S	8.3	6.1	17.6	8.6	0.271
(58) *One-KPNA-422*	S	8.0	7.0	13.9	9.3	0.038
(59) *One-U502–167*	S	7.6	7.1	13.4	9.3	0.063
(60) *One-MARCKS-241*	S	7.0	6.6	15.1	10.1	0.036
(61) *One-E2*	S	5.1	5.7	12.0	8.8	0.015
(62) *One-CYTB-17*	SM	2.3	3.2	7.5	5.6	—
(63) *One-CYTB-26*	SM	2.3	3.2	7.5	5.6	—
(64) *One-CO1*	SM	2.3	3.2	7.5	5.6	—

Note: Types: M, microsatellites; MHC, major histocompatibility complex; S, single nucleotide polymorphisms (SNPs); SM, mtDNA SNPs.

Subsequent analyses were conducted exclusively with ONCOR. Single-population samples were analyzed with 10, 15, 20, 25, 30, 35, 40, and 46 SNPs. SNPs with the highest average accuracy were initially incorporated in the analyses of the single-population mixtures, with lower-accuracy SNPs sequentially added to the analyses. Average population accuracy and precision were recorded for each set of SNPs. Additionally, SNPs with the lowest average accuracy values were initially incorporated in the analyses, with progressively higher-accuracy SNPs sequentially added to the analyses, again with average accuracy and precision recorded. Overall mean accuracy and precision for each specified number of SNPs were determined by averaging the results from both processes, and this was considered indicative of the average trend in estimating accuracy and precision when the number of SNPs employed in the analysis was increased. Average regional, population, and individual accuracy and precision over all 44 populations were recorded for each set of SNPs. A hyperbola function of the form $Y = a/X + b$ was fitted with LAB Fit curve fitting software (da Silva and da Silva 2007), with the number of SNPs incorporated in the analysis as the independent variable X, and mean observed accuracy for population and regional estimates as the dependent variable Y. Estimates of standard deviations were fitted with an inverse straight-line equation $Y = 1/(aX + b)$, with X and Y as previously defined. Population and regional individual assignment accuracy were fitted with an inverse hyperbola equation $Y = X/(a + bX)$, with X and Y as previously defined. Projections were then made with these regression models to estimate the number of SNPs that would be required to provide estimates of resolution comparable with that provided by the microsatellites with respect to estimated stock compositions at both the regional and population level, as well as individual identification to the regional and population level.

Results

Population sample size

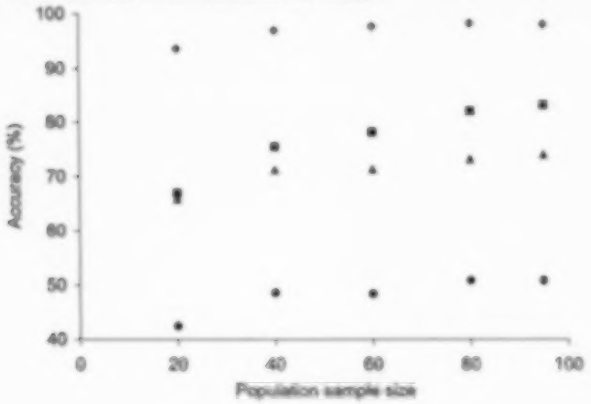
Average realized population sample sizes were 97 individuals successfully genotyped at SNP loci, 254 individuals at the MHC locus, and 292 individuals at the microsatellite loci (Table 1). Sample size variation was limited at SNPs, ranging from an average of 71 to 370 individuals successfully genotyped. Sample size variation was more variable at the MHC locus, ranging from 31 to 785 individuals genotyped. The most extensive sample size variation was observed at the microsatellites, ranging from 85 to 1687 individuals genotyped at individual populations. The most extensive population survey was conducted for the Cultus Lake population, as this is the population of highest conservation concern in the Fraser River drainage.

For SNPs, 97 individuals were genotyped, on average, to estimate the population frequency of one independent allele, with 254 individuals genotyped to estimate population frequency of 11 independent alleles for the MHC locus and with 292 individuals genotyped to estimate population frequency of an average of 29 independent alleles at microsatellites. Once approximately 95 individuals had been sampled for SNP variation within a population, there was virtually no increase in accuracy of estimated stock compositions or individual assignment (Fig. 2). Thus, even though the number of individuals genotyped was the smallest for SNPs, intermediate for MHC, and greatest for microsatellites, variation in population sample size should have no marked effect on the relative performance of the different marker classes.

Relative ranking of the markers

Average population-specific accuracy for the 64 markers evaluated ranged from 81.2% to 2.3%, with a clear break in accuracy observed between microsatellites and SNPs. The top 15 markers of the 64 markers evaluated were either microsatellites or MHC, with accuracy of estimated population-specific stock compositions produced from incorporating the worst microsatellite (*Oki1b*) approximately double that of the highest ranked SNP (*One-MHC2–190*) (34.6% versus 16.0%) (Table 2). Similar results were observed for region-specific accuracy (45.4% versus 27.7%) for the two loci. F_{ST} value was a poor predictor of the relative value of each marker for stock composition analysis. Markers with higher F_{ST} values, such as the MHC β1 locus (0.245) and the SNP locus *One-MHC2–190* (0.307) did not provide as much population-specific resolution as did nine microsatellites with lower F_{ST} values (0.028–0.141) (Table 2). Two SNPs with F_{ST} values > 0.25 were not

Fig. 2. Effect of population sample size for SNPs on average accuracy of estimated stock compositions for both population-specific (■) and regional estimates (◆), as well as individual assignment accuracy to population (●) and region (▲).



among the top five SNP loci evaluated, even though the F_{ST} values of the top five SNPs ranged from 0.21 to 0.31. For *One-RH2OP-395*, allele frequencies were markedly different from the norm (dominant allele frequency 0.89–1.00) for only one population (Cultus Lake, allele frequency 0.34), and for *One-STC-410*, allele frequencies were markedly different from the norm (dominant allele frequency 0.74–1.00) for three central coastal populations (Devon Lake, Kent Lake, and Tankeeah River, allele frequency range 0.38–0.47). These four populations were already well differentiated from other populations at other loci (Tables 1, 3), so no loss of stock composition resolution was incurred by not incorporating these two SNP loci into the group of the top five SNPs.

Heterozygosity was also a poor predictor of the relative power of each marker for stock composition analysis. For microsatellites, there were only minor differences in accuracy of estimated stock compositions for loci with a heterozygosity value > 0.60 (Fig. 3*a*). Similarly, there were only minor differences among SNPs for loci with a heterozygosity value > 0.10 (Fig. 3*b*). The mtDNA SNP markers were the poorest of all markers surveyed in terms of providing accurate population-specific estimates of stock composition (Table 2).

How many SNPs for MHC equivalency?

Average stock composition of the single-population samples incorporating 14 microsatellites and the MHC locus was 92.4% when estimated with SPAM and 85.8% when estimated with ONCOR. These levels of accuracy provided the reference points when evaluating the equivalency between SNPs and MHC when used in conjunction with microsatellites to estimate sockeye salmon stock composition. Sequential addition of the five highest rated SNPs to the suite of 14 microsatellites provided the equivalent average accuracy to analyses with microsatellites and MHC (SPAM, 92.3%; ONCOR, 86.0%) (Table 1). Two of the top five SNPs were derived from MHC sequences.

Population-specific accuracy differed only modestly between SPAM and ONCOR when the populations were well defined, as populations estimated with greater than 90% accuracy in SPAM were generally estimated with greater than 90% in ONCOR. However, for those populations that were less well defined (SPAM estimate less than 90%), estimated stock compositions derived from SPAM were consistently higher than those derived from ONCOR (Table 1).

How many microsatellites for SNP equivalency?

The application of 46 SNPs to estimate stock composition of 44 single-population samples resulted in an average accuracy of 83.5% to population (Table 3). Individual population estimates ranged from 54.3% for the Takla Lake population to 99.9% for the Cultus Lake population. Starting with the microsatellite with highest observed population-specific accuracy (*Ots100*), an average level of accuracy of 82.9% was achieved by incorporating the best six microsatellites. There was no significant difference in population-specific accuracy estimated from the 46 SNPs or six microsatellites, with accuracy of estimated stock compositions derived from these six microsatellites greater than those derived from the 46 SNPs for 20 of the populations and less than those for 24 populations (sign test analysis, $P > 0.10$). The average population-specific accuracy for estimates incorporating all 14 microsatellites was 85.5%. Estimates produced by incorporating 14 microsatellites were significantly more accurate than those produced incorporating 46 SNPs, with microsatellite-based estimates greater than those derived from SNPs for 32 populations and less than those for 12 populations ($P < 0.01$). Some populations such as Cultus Lake, Chilliwack Lake, and Gates Creek were clearly more differentiated than others, with high levels of population-specific accuracy (>97%), regardless of what suite of markers was used to estimate stock composition. Similarly, estimated stock compositions for populations that displayed lower levels of accuracy such as Lower Horsefly River were consistently lower with both microsatellites and SNPs.

The application of 46 SNPs for estimation of standard deviation in 44 single-population samples resulted in an average standard deviation of 4.4% to population (Table 4). Individual population estimates ranged from 0.1% for the Cultus Lake population to 11.7% for the Takla Lake population. The average standard deviation of the estimated stock compositions for the top five microsatellites was 4.2%. There was no significant difference in standard deviation estimated from the 46 SNPs or five microsatellites, with standard deviations of estimated stock compositions derived from these five microsatellites less than those derived from the 46 SNPs for 24 of the populations and greater than for 20 populations (sign test analysis, $P > 0.05$). The average population-specific standard deviation for estimates incorporating all 14 microsatellites was 3.2%. Estimates produced by incorporating 14 microsatellites were significantly more precise than those produced incorporating 46 SNPs, with microsatellite-based standard deviations less than those derived from SNPs for 42 populations and greater than those for two populations ($P < 0.01$).

The application of 46 SNPs to assignment of individual fish resulted in an average correct assignment of 50.8% to population and 74.4% to region (Table 4). Population assignment accuracy ranged from 10.1% for the Seymour Creek population to 98.4% for the Cultus Lake population

Table 3. Mean accuracy and precision of estimated stock compositions of single-population samples, as well as percentage correct individual assignment to specific populations and region, for a suite of six microsatellites (*Ots100*, *Oki16*, *Oki29*, *Ots108*, *Oki10*, *Ots103*) and suite of 46 SNPs (the top 46 from Table 2), with accuracy, precision, and percentage allocation estimated from ONCOR over 44 sockeye salmon populations from British Columbia. Populations within regions are described in Table 1.

			Accuracy (%)		Precision (%)		Individual assignment (%)	
Region	Population	Type	Population	Region	Population	Region	Population	Region
Upper Fraser	Bowron Lake	M	96.53	96.76	1.77	1.77	70.1	70.1
		S	98.62	98.62	1.02	1.02	80.0	80.0
Early Stuart	Takla Lake	M	54.26	98.28	8.49	1.16	38.7	66.9
		S	62.76	97.01	11.65	2.41	32.6	60.6
Early Stuart	Trembleur Lake	M	70.88	98.12	8.04	1.49	36.2	66.6
		S	86.77	98.67	8.42	1.59	43.5	71.8
Late Stuart	Stellako River	M	93.26	98.47	2.85	1.16	48.8	73.1
		S	82.21	98.74	5.70	1.28	41.7	84.7
Late Stuart	Middle River	M	89.30	95.64	4.03	2.19	45.2	67.8
		S	73.42	92.79	6.22	3.87	44.2	69.8
Late Stuart	Nadina River	M	97.82	99.25	1.46	0.68	70.3	84.9
		S	97.67	99.41	1.88	0.85	62.7	84.0
Late Stuart	Pinchi Creek	M	49.25	93.53	5.47	2.77	26.0	64.9
		S	70.36	97.70	7.13	2.06	25.4	81.0
Chilko	Chilko River	M	90.94	96.58	3.99	0.17	35.0	50.8
		S	83.05	96.62	4.85	1.73	38.1	66.7
Chilko	Chilko Lake south	M	89.38	97.83	4.04	1.36	53.2	66.8
		S	86.46	98.73	5.59	1.06	48.6	70.3
Quesnel	Mitchell River	M	91.21	99.88	3.15	0.23	80.1	98.9
		S	86.56	99.38	4.89	0.52	70.4	85.2
Quesnel	Lower Horsefly	M	37.80	97.98	7.22	1.29	18.8	71.0
		S	41.27	97.71	8.18	1.74	26.0	70.0
Quesnel	Upper Horsefly	M	70.28	98.87	7.94	1.00	26.9	78.6
		S	49.40	97.24	8.90	1.34	16.1	71.0
Quesnel	McKinley Creek	M	39.84	98.45	8.34	1.15	33.3	79.7
		S	60.28	98.56	8.49	1.07	31.1	67.2
Quesnel	Blue Lead Creek	M	74.17	98.85	5.13	0.79	39.5	78.9
		S	81.33	97.44	4.94	1.47	21.4	78.6
Canyon	Gates Creek	M	99.35	99.42	0.60	0.59	93.6	94.2
		S	99.68	99.72	0.35	0.32	91.1	91.1
Canyon	Nahatlatch River	M	99.07	99.20	0.67	0.67	89.8	90.4
		S	98.88	98.89	0.80	0.80	76.4	77.8
Harrison	Birkenhead River	M	98.11	98.55	1.15	0.80	75.6	82.1
		S	99.09	99.45	0.51	0.43	73.3	86.7
Harrison	Weaver Creek	M	98.30	99.02	1.15	0.70	70.7	79.3
		S	99.02	99.46	1.06	0.55	83.3	91.7
Harrison	Harrison River	M	96.13	97.41	1.77	1.38	50.4	58.0
		S	98.53	99.18	0.90	0.67	76.5	88.2
Harrison	Big Silver Creek	M	98.80	98.94	0.98	0.87	79.2	85.5
		S	97.08	97.73	1.59	1.29	69.4	76.4
Lower Fraser	Pitt Lake	M	98.54	98.54	0.83	0.83	73.4	73.4
		S	97.88	97.88	1.62	1.62	64.7	64.7
Chilliwack	Cultus Lake	M	99.85	99.86	0.26	0.22	95.8	96.6
		S	99.98	99.98	0.11	0.08	98.4	98.4
Chilliwack	Chilliwack Lake	M	99.78	99.80	0.39	0.31	97.6	98.8
		S	99.92	99.93	0.17	0.15	92.3	92.3
North Thompson	Fennell Creek	M	97.02	99.39	2.18	0.59	70.3	88.3
		S	96.98	98.28	1.78	1.14	50.0	57.4
North Thompson	Raft River	M	89.97	98.81	3.49	0.93	50.8	78.5
		S	78.36	96.05	6.34	2.01	31.0	60.6
North Thompson	North Thompson	M	87.15	93.85	4.18	2.55	51.0	68.8
		S	79.37	92.38	5.63	3.32	17.1	32.9

Table 3 (*concluded*).

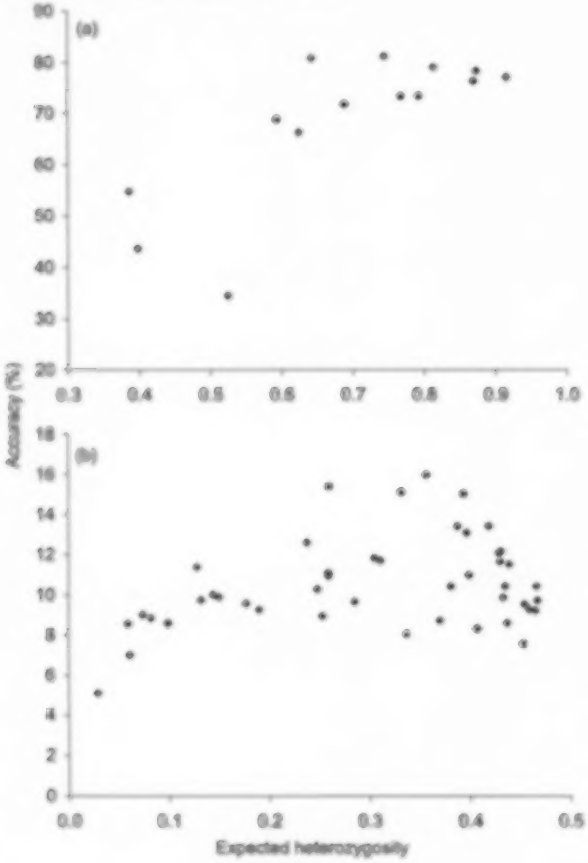
Region	Population	Type	Accuracy (%)		Precision (%)		Individual assignment (%)	
			Population	Region	Population	Region	Population	Region
Shuswap Early	Scotch Creek	M	88.44	99.07	4.08	0.98	58.5	79.3
		S	78.29	97.16	5.69	1.73	30.9	57.4
Shuswap Early	Eagle River (early)	M	93.98	99.22	2.51	0.69	50.3	88.7
		S	89.46	98.87	4.53	0.90	45.9	73.0
Shuswap Early	Seymour Creek	M	82.04	96.44	5.12	2.16	36.4	77.7
		S	72.90	94.75	6.13	2.72	10.1	47.8
Shuswap Early	Upper Adams River	M	97.08	98.83	1.72	0.79	62.3	88.1
		S	91.38	99.07	3.84	0.82	40.9	79.5
Shuswap Early	Cayenne Creek	M	92.80	99.99	2.45	0.04	91.7	100.0
		S	92.45	99.74	3.97	0.46	63.6	84.8
Shuswap Late	Lower Adams River	M	78.77	93.85	5.44	2.63	19.1	46.4
		S	84.91	95.33	4.39	2.37	12.2	48.8
Shuswap Late	Lower Shuswap	M	55.99	97.85	6.49	1.32	28.2	76.3
		S	68.12	96.82	6.70	2.11	25.4	54.0
Shuswap Late	Middle Shuswap	M	71.29	98.60	6.11	1.06	34.7	70.5
		S	71.05	98.49	6.78	1.05	23.1	50.0
Shuswap Late	Eagle River (late)	M	66.74	96.54	5.43	2.04	44.2	68.6
		S	84.07	96.98	5.28	1.98	29.8	61.7
South Coast	Phillips River	M	98.72	98.72	0.84	0.84	90.4	90.4
		S	99.78	99.78	0.34	0.34	95.1	95.1
Long Lake	Smokehouse Creek	M	59.43	96.27	5.96	1.70	41.0	85.9
		S	69.47	99.57	7.67	0.67	48.3	75.9
Long Lake	Canoe Creek	M	60.43	98.72	6.15	0.89	39.6	69.4
		S	71.02	98.83	7.72	1.22	45.6	78.9
Owikeno	Washwash River	M	69.94	98.93	6.47	0.74	40.7	81.9
		S	72.14	99.11	6.46	0.80	39.1	76.8
Owikeno	Neechanz River	M	64.79	98.58	6.68	0.91	32.8	77.2
		S	64.76	98.23	7.95	1.24	34.3	68.6
Owikeno	Sheemahant River	M	62.41	98.53	6.20	0.90	31.5	76.6
		S	59.89	98.03	7.41	1.26	23.0	68.9
Central Coast	Devon Lake	M	99.05	99.26	0.84	0.81	88.6	90.9
		S	99.83	99.87	0.26	0.18	85.4	95.1
Central Coast	Tankeeah River	M	98.93	99.15	0.86	0.83	88.7	92.1
		S	99.65	99.90	0.51	0.21	90.7	97.3
Central Coast	Kent Lake	M	99.54	99.77	0.55	0.33	91.8	94.1
		S	99.81	99.97	0.36	0.14	87.9	100.0
Mean		M	82.89	98.15	3.72	1.11	56.6	78.8
		S	83.47	98.13	4.43	1.24	50.8	74.4

(Table 3). Regional assignment accuracy ranged from 32.9% for the North Thompson River population to 100% for the Kent Lake population. Comparable population-specific levels of assignment accuracy were achieved with an application of five microsatellites (52.5%), with comparable levels of regional assignment accuracy achieved also with five microsatellites (70.1%) (Table 4). In summary, the application of the best six microsatellites produced levels of population-specific and regional accuracy and precision for estimates of stock composition, as well as levels of correct individual assignment to population and region, comparable with those produced by application of the best 46 SNPs.

How many SNPs for microsatellite equivalency?

Average stock composition accuracy of the single-population samples incorporating 14 microsatellites was 85.53% to a specific population and 99.20% to geographic region (Table 5). Standard deviations of the estimates were 2.94% and 0.61%, respectively. Average accuracy of individual assignment was 67.71% to specific population and 91.48% to region. These levels of accuracy, precision, and individual assignment provided the reference points for estimation of the number of SNPs required to provide equivalent results in stock identification applications as derived with the microsatellites. The estimated number of SNPs required to provide equivalent results to those of the microsatellites depended on the complexity of the task. The easiest task, estimation of regional stock composition, was estimated to require 53 SNPs of the average quality evaluated in the study to provide equivalent levels of accuracy as that observed with the microsatellites (Table 6; Fig. 4). However, equivalent precision in regional estimates of stock composition was estimated to require 104 SNPs of the quality evaluated in the study (Table 6; Fig. 4). Thus,

Fig. 3. (*a*) Accuracy of stock composition estimation of single-population samples versus microsatellite heterozygosity for sockeye salmon in British Columbia; (*b*) accuracy of stock composition estimation of single-population samples versus SNP heterozygosity for sockeye salmon in British Columbia.



53–104 SNPs were projected to be required to provide accuracy and precision of estimated regional stock compositions equivalent to the microsatellites.

The next most difficult task was determination of population-specific estimates of stock composition. Equivalent accuracy in population-specific estimates of stock composition was estimated to require 75 SNPs of the quality evaluated in the study, whereas equivalent precision was estimated to require 79 SNPs (Table 6; Fig. 4). Thus, 75–79 SNPs were projected to provide accuracy and precision of estimated population-specific stock compositions equivalent to the microsatellites.

The most difficult task in stock identification applications is the assignment of individuals to specific groups, with correct assignment to a region obviously easier to obtain than correct assignment to an individual population within a region. Equivalency in assignment accuracy to region was estimated to require 100 SNPs of the quality evaluated in the study, whereas equivalent accuracy in assignment to specific populations was estimated to require 124 SNPs (Table 6; Fig. 4). Clearly, the number of SNPs required to provide results of a quality equivalent to that of the existing suite of microsatellites depends on the complexity of the application.

Discussion

Sample size

SNPs typically display two alleles at a locus, but if the frequency of one allele is determined, then the frequency of the other allele is known as well. Thus, SNPs display one independent allele per locus. The other types of markers surveyed in the study (MHC and microsatellites) display multiple independent alleles per locus, with the microsatellites displaying up to 84 independent alleles per locus. Comparison of the efficacy of SNPs and microsatellites for stock identification applications requires that adequate sample sizes be available for populations included in the analyses for both classes of markers. Clearly, highly polymorphic microsatellites require more fish to be sampled in a population to obtain estimates of allele frequencies with similar accuracy and precision compared with SNPs, where the frequency of only one independent allele is estimated. T.D. Beacham, B. McIntosh, and C. Wallace (unpublished data) demonstrated that microsatellites required larger baseline sample samples than SNPs to reduce sampling variation in estimation of allele frequencies and thus increase accuracy of estimated stock compositions. Population sample size in the microsatellite baselines was required to be about two to three times larger than in the SNP baselines before equivalent levels of accuracy relative to the asymptotic value were obtained. Therefore, in comparing the effectiveness of SNPs and microsatellites for stock identification estimation for Pacific salmon, larger baseline population sample sizes will be required for microsatellites than for SNPs for all species.

Studies of salmonid population structure and stock identification incorporating nuclear SNPs typically include sample sizes of approximately 95 individuals per population (Smith et al. 2005*b*; Narum et al. 2008; Smith and Seeb 2008), and our study utilized the same experimental approach. Simulation modeling showed that once approximately 95 individuals had been sampled at SNP loci within a population, there was virtually no increase in accuracy of estimated stock compositions or individual assignment. Thus, accuracy of estimated stock compositions and assignment of individuals derived from SNPs was not limited by population sample size in our study. Estimates of stock composition of single-population samples of salmon derived from microsatellites can be limited by population sample size, with population sample sizes of approximately 200 individuals required before there is little effect of sample size on accuracy of population-specific estimates (Beacham et al. 2006*c*). However, as population sample sizes for microsatellites of most populations in the study were greater than 200 fish, accuracy of estimated stock compositions and assignment of individuals derived from microsatellites was also not significantly limited by population sample size in our study (T.D. Beacham, B. McIntosh, and C. Wallace, unpublished data).

Relative ranking of the markers

Several methods are available to measure the information content of genetic markers for population differentiation and

Table 4. Mean estimated population and regional stock composition (% accuracy) of single-population samples determined from ONCOR from suites of markers incorporating the best 3, 4, 5, 6, 7, 8, 10, 12, and 14 microsatellites (micros) from Table 2, as well as the best 46 SNPs. Percent correct assignment of individuals to specific populations and regions is also indicated.

	Stock composition (%)		Standard deviation (%)		Individual assignment (%)	
Loci	Population	Region	Population	Region	Population	Region
3 micros	79.85	96.39	5.67	1.93	40.63	60.28
4 micros	81.05	97.50	4.72	1.48	47.96	69.55
5 micros	81.57	97.81	4.02	1.27	52.50	74.05
6 micros	82.89	98.15	3.72	1.11	56.61	78.80
7 micros	84.00	98.40	3.63	0.98	59.52	82.68
8 micros	84.37	98.71	3.35	0.86	62.05	85.73
10 micros	84.84	98.96	3.14	0.74	65.06	88.73
12 micros	85.38	99.12	2.98	0.65	66.30	90.25
14 micros	85.53	99.20	2.94	0.61	67.71	91.48
46 SNPs	83.47	98.13	4.43	1.24	50.83	74.38

Table 5. Mean estimated population and regional stock composition (% accuracy) and precision (standard deviation, %) of single-population samples determined from ONCOR from suites of markers incorporating the best 10, 15, 20, 25, 30, 35, 40, and 46 SNPs from Table 2, as well as all 14 microsatellites. Percent correct assignment of individuals to specific populations and regions is also indicated.

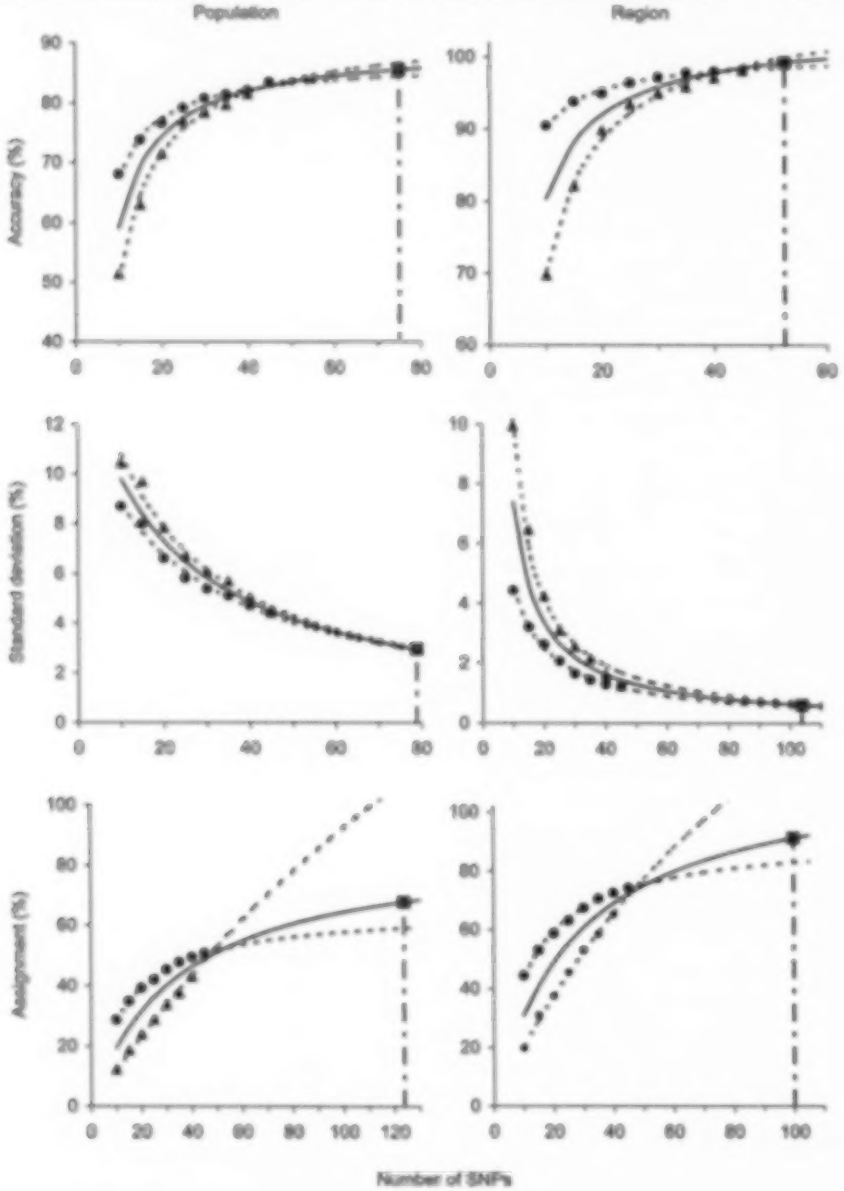
	Stock composition (%)		Standard deviation (%)		Individual assignment (%)	
Loci	Population	Region	Population	Region	Population	Region
10 SNPs	68.05	90.47	8.69	4.44	28.68	44.46
15 SNPs	73.82	93.82	8.00	3.21	34.86	53.06
20 SNPs	76.61	94.98	6.62	2.62	39.36	58.78
25 SNPs	79.19	96.41	5.82	2.07	41.97	63.08
30 SNPs	80.77	97.17	5.38	1.65	45.35	67.47
35 SNPs	81.44	97.79	5.10	1.44	47.82	70.63
40 SNPs	82.11	98.01	4.71	1.30	49.48	72.60
46 SNPs	83.47	98.13	4.43	1.24	50.83	74.38
14 micros	85.53	99.20	2.94	0.61	67.71	91.48

Table 6. Estimated number of SNPs required to equal performance of 14 microsatellites with respect to accuracy and precision (SD) of population and regional estimates of stock composition, as well as percentage correct individual assignment to population and region, based on fitting functions to results outlined in Table 5. The proportion of variance accounted for by fitting each function (r^2) is also listed.

Class	Population	r^2	Region	r^2
Accuracy	75	0.9954	53	0.9964
Precision	79	0.9855	104	0.9961
Individual assignment	120	0.9931	100	0.9953

individual assignment (Rosenberg et al. 2003; Hedrick 2005). The basis for much of the work on genetic variation in Pacific salmon is to develop a baseline for stock identification application. As such, our measure of the relative ranking of markers was based solely on their observed accuracy in stock identification. Narum et al. (2008), in a study evaluating the effectiveness of 13 microsatellites and 37 SNPs in 29 Chinook salmon populations, reported that the best 10 loci for correct individual assignment were microsatellites, and that the best 15 loci included 12 microsatellites and three SNPs. The top 15 markers of the 64 markers evaluated in our study were either microsatellites or MHC, with accuracy of estimated population-specific stock compositions produced from incorporating the least informative microsatellite approximately double that of the highest ranked SNP. The number of alleles observed at each microsatellite locus ranged from 7 to 85, with an average of 30 alleles per locus. Microsatellites containing only a few alleles (<five) were not included in our analyzed suite, as we recognized early in locus selection that such loci provide limited stock resolution. This was illustrated by Beacham et al. (2005c): the number of alleles observed at a locus was generally related to the power of the locus in providing accurate estimates of stock composition. Thus, the microsatellites included in the current suite did undergo some initial evaluation in the 1990s, but the 14 microsatellites in the current baseline were simply 14 microsatellites that initially displayed enough polymorphism to be considered for inclusion in a suite of microsatellites, were in Hardy–Weinberg equilibrium in test populations, and now fit on two injections for an automated DNA sequencer. The current suite was first used for individual assignment to three lakes in Barkley Sound on the west coast of Vancouver Island (Beacham et

Fig. 4. Accuracy and standard deviations of regional and population estimates of stock composition versus number of SNPs employed in estimation procedure, as well as accuracy of individual assignment to specific regions or populations. The number of SNPs projected to be required to provide results comparable with those of 14 microsatellites is indicated (■ and continuous curve). Estimates were bounded by initially incorporating SNPs with the highest average accuracy in the analyses of the single-population mixtures, with lower-accuracy SNPs sequentially added to the analyses. Average population accuracy and precision were recorded for each set of SNPs (● and dotted line). Subsequently, SNPs with the lowest average accuracy values were initially incorporated in the analyses, with progressively higher-accuracy SNPs sequentially added to the analyses, again with average accuracy and precision recorded (▲ and broken line). Overall mean accuracy and precision for each specified number of SNPs were determined by averaging the results from both processes and used in projections.



al. 2002) and for in-season stock identification of Fraser River sockeye salmon in 2002 (Beacham et al. 2004*a*).

How many SNPs for MHC equivalency?

One of the objectives of the current study was to evaluate the number of SNPs that were required to replace the MHC locus in GSI applications for Fraser River sockeye salmon with no loss of average population resolution. Replacement of the MHC locus with SNPs allows more synchronous availability of laboratory results with the microsatellites.

The best five SNPs were demonstrated to provide equivalent GSI resolution to the MHC locus, and these SNPs were chosen to replace the power provided by MHC in Fraser River sockeye salmon GSI applications. Incorporation of known linkage between the two MHC SNPs in stock identification analysis may also provide increased resolution in stock composition estimates beyond that observed in the current study. Although an all-SNP approach to Pacific salmon GSI applications was implied by PSC (2005), this change would currently appear to be of questionable merit at this time. Instead, an approach that harnesses the existing power of a combined microsatellite–SNP approach would seem to be the best current technique available for Fraser River sockeye salmon GSI applications. Inclusion of both microsatellites and SNPs in a suite of loci for Chinook salmon individual assignment was also the approach recommended by Narum et al. (2008).

Stock compositions of simulated single-population samples displayed little difference between those estimated by SPAM and ONCOR when populations were well differentiated from other populations. However, among closely related populations, estimates derived from SPAM were higher than those estimated with ONCOR. Anderson et al. (2008) reported that stock compositions derived from SPAM can overestimate the predicted accuracy of stock compositions for closely related populations relative to estimates derived from ONCOR, and the results from the current study support this conclusion.

Microsatellites or SNPs?

If better stock ID resolution is required for southern British Columbia sockeye salmon in the existing SNP and microsatellite databases, is it more effective to add SNPs or microsatellites? Morin et al. (2009) suggested that SNPs may offer significant advantages over microsatellites, including lower error genotyping rates, less effort in data standardization, possible incorporation of variation in coding regions of DNA, and technologies for high throughput genotyping. Smith and Seeb (2008) suggested that comparable amounts of effort spent on developing SNP and microsatellite baselines will result in SNP baselines with greater information content per allele. In most applications, SNP alleles will likely have higher information content per allele. In the current study, the top six microsatellites provided equivalent power to the 49 SNPs evaluated. The top six microsatellites displayed 245 alleles, whereas the 49 SNPs displayed 98 alleles (49 independent), illustrating that SNP alleles provided greater information content per allele. Although the relative power of individual alleles is of some interest, a more salient, practical concern is the number of loci for each class of markers that must be analyzed to provide comparable results. The number of loci required in each class of markers for comparable stock identification results is vital to determine, as this will largely determine the cost per individual in subsequent analysis. Vignal et al. (2002, p. 299) suggested that with the progress being made in identifying and surveying SNP variation, "the effort needed to produce an equivalent amount of information as with microsatellites may some day be equivalent." The question evaluated in the current study was whether that day has arrived for sockeye salmon stock identification in British Columbia.

The results of the current study indicated that additional SNPs would be required to be surveyed to provide the equivalent stock identification power as the existing microsatellites. Considerable effort would be required for SNP discovery to enhance the baseline evaluated in our study, as all known reported SNPs for sockeye salmon were incorporated in the survey. For microsatellites, the worst-performing locus provided twice the average population-specific mean accuracy than the best-performing SNP. The current suite of microsatellite loci was developed about 10 to 15 years previously, and there are now literally hundreds of microsatellites available for salmonids. Many microsatellites are easily transferrable among species, and a broad range of microsatellites could be screened rapidly in test populations. Microsatellites specifically chosen for their stock separation of southern British Columbia sockeye salmon could then be incorporated into existing SNP or microsatellite baselines. If additional stock identification resolution is required, the cost of incorporating a third injection on an automated DNA sequencer would have to be compared with the costs of surveying an unknown number of SNPs above the 124 currently estimated as required to provide equivalency with the power of the existing suite of microsatellites.

Suppose that sufficient resolution in stock identification estimates is provided for some applications by the 45 SNPs in the suite used in applications in Alaska. If so, the analysis presented herein suggests that equivalent resolution would likely be provided by applying the best six microsatellites currently used in applications in British Columbia and northern Washington. However, it is uncertain if the existing set of SNPs has the same relative population separation power in other areas of the species distribution, e.g., Russia. New SNPs may have to be incorporated for stock identification applications in those regions. The 14 microsatellites analyzed in the current study have already been demonstrated to be of considerable value in stock composition estimation in Russia (Beacham et al. 2006*b*), Southeast Alaska and northern British Columbia (Beacham et al. 2005*a*), central British Columbia (Beacham et al. 2005*b*), and southern British Columbia and Washington (Beacham et al. 2004*a*, 2004*b*), as well as on a Pacific Rim basis (Beacham et al. 2005*c*). The current analysis indicated that up to 124 SNPs would be required to equal the power of stock identification applications centering on Fraser River sockeye salmon available from the 14-microsatellite baseline. Pacific Rim stock identification applications conducted solely with SNPs may require more than the 124 SNPs estimated to provide equivalency for Fraser River sockeye salmon applications, possibly in excess of 150 SNPs may be required to provide the same degree of resolution available at the individual identification level as available with the 14 microsatellite baseline.

Will discovery of a number of new SNPs in sockeye salmon over and above those evaluated in this study fundamentally change the relative power of microsatellites and SNPs for stock identification? In human genomics research, over three million SNPs have been discovered (International HapMap Consortium 2007). Advocates of a SNP-only method of stock identification in fisheries frequently claim that advancements in human genomics research will render application of SNPs the preferred approach in fisheries stock

identification. This view was typified by PSC (2005, p. 128), where it was noted that "the human genetics community has already undergone a transition from microsatellite to SNP markers". The implication is that advances are made first in human genetics research, which are then applied by investigators in other fields such as fisheries stock identification. Gill et al. (2004), outlining the consensus of a working group of European and American forensic scientists, assessed whether SNPs will replace STRs (short tandem repeats, i.e., microsatellites) in human forensic investigations. They noted: "It is easy to be swept along in the tide of new technology, simply because it is something different. However, we must take a step back and objectively evaluate the reasons for implementing a new system. New does not necessarily mean better. We should remember that SNPs were initially developed for forensic application in the late 1980s and early 1990s, but were superseded by STRs (microsatellites) because of their marked superiority — the discussion is not new" (Gill et al. 2004, p. 51). In an evaluation of microsatellites (STRs) and SNPs for human forensic applications, Butler et al. (2007, p. 203) concluded that "we do not feel that SNPs stand on the horizon as future markers (i.e., replacing STRs) for widespread use in forensic DNA testing". In spite of a suite of over three million SNPs from which to choose, human forensic investigators concluded that microsatellites would be the dominant technology employed for the foreseeable future. If indeed human applications provide the path for future fisheries stock identification, then SNP-only applications in fisheries GSI work may be best reserved for those situations and laboratories in which microsatellites cannot be applied efficiently, given the number of SNPs that must be analyzed to provide GSI resolution comparable with that of existing suites of microsatellites.

Butler et al. (2007) noted that several significant disadvantages exist with SNP markers when considered as a possible replacement for the currently used set of 13–15 microsatellites for human forensic applications. These disadvantages are directly analogous to fisheries stock identification applications. Because SNPs are not as polymorphic as microsatellites, more SNPs are required to provide equivalent powers of discrimination, they have less ability to decipher mixtures, and the expense of screening more SNPs for each sample will be higher as compared with microsatellites (Butler et al. 2007). The microsatellites employed in human forensic studies are routinely amplified in a single multiplex amplification reaction. Cost of laboratory analysis for an individual fish is a key issue in deciding the appropriate technology to apply in a particular laboratory. In our laboratory, after DNA has been extracted from a sample, the laboratory cost of analysis incurred for sockeye salmon incorporates eight polymerase chain reaction (PCR) amplifications of the 14 microsatellites and then sizing the amplified products on two injections on an automated DNA sequencer. For this technology to be replaced, as was implied by PSC (2005), it must be demonstrated that SNPs provide either equivalent performance at a cheaper analytical cost per fish than that obtained with microsatellites or enhanced stock identification capability at the same analytical cost per fish. To date, much like forensic applications in human genetics, a SNP-only approach to sockeye salmon GSI applications in our laboratory fails to meet either requirement. Technologies are replaced when one technique provides a clear advantage over the other, e.g., replacement of allozymes by microsatellites or SNPs as the main technique employed to survey genetic variation in Pacific salmon. The estimated number of SNPs required to provide equivalent GSI resolution and individual assignment to that of the microsatellites ranged from approximately 53 to 124 SNPs, depending on the degree of difficulty of the application. Although a number of techniques are available for the survey of SNP variation, we are aware of no technique that will allow up to 124 SNPs to be analyzed at a cost comparable with analyzing 14 microsatellites in eight PCR amplifications coupled with two injections on an automated DNA sequencer. A combination of microsatellites and a limited number of SNPs would currently appear to be the best strategy employed for sockeye salmon GSI applications in British Columbia at the present time. Indeed, this was the strategy employed in applications in southern British Columbia in 2009, with 14 microsatellites and the top five SNPs applied in real-time estimation of sockeye salmon stock composition from test and commercial fisheries.

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Are seasonal lakes as productive as permanent lakes? A case study from Ireland

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Abstract: This paper compares, for the first time, nutrient levels and chlorophyll *a* measured in a set of seasonal lakes with those reported for permanent lakes in the literature. Twenty-two turloughs (karstic seasonal lakes) in western Ireland were sampled monthly from the onset of flooding (October) until they dried out (6 to 9 months). The turloughs showed similar levels of nutrients and chlorophyll *a* to those reported for Irish and international lakes. Chlorophyll *a* peaked between November and February in the majority of turloughs, sometimes with values higher than those measured in mesotrophic lakes in summer. A significant log-linear regression was found between total phosphorus and chlorophyll *a*, which suggests P limitation of algal biomass in the majority of the turloughs. The regression characteristics were not significantly different than those described in similar studies of permanent lakes. Patterns in seasonal variation of nutrients are also presented, their underlying causes being discussed in relation to their transport within catchments. Our results show that despite being predominantly winter phenomena, turloughs can be as productive as permanent lakes.

Résumé : Notre travail compare pour la première fois les concentrations de nutriments et de chlorophylle *a* dans une série de lacs saisonniers à celles rapportées dans la littérature pour les lacs permanents. Nous avons échantillonné à chaque mois 22 turloughs (lacs karstiques saisonniers) dans l'ouest de l'Irlande jusqu'à leur assèchement (6 à 9 mois). Les turloughs ont des concentrations de nutriments et de chlorophylle *a* semblables à celles signalées dans les lacs irlandais et les lacs ailleurs dans le monde. La chlorophylle *a* atteint un pic entre novembre et février dans la majorité des turlougs, dépassant quelquefois les valeurs mesurées dans les lacs mésotrophes en été. Il existe une régression linéaire logarithmique significative entre le phosphore total et la chlorophylle *a*, ce qui semble indiquer une limitation de la biomasse algale par le P dans la majorité des turloughs. Les caractéristiques de la régression ne sont pas significativement différentes de celles décrites dans des études semblables de lacs permanents. Nous présentons les patrons de variation saisonnière des nutriments et discutons de leurs causes sous-jacentes en relation avec leur transport au sein des bassins versants. Nos résultats montrent que, bien qu'ils soient surtout des phénomènes hivernaux, les turloughs peuvent être aussi productifs que les lacs permanents.

[Traduit par la Rédaction]

Introduction

The current knowledge on the ecology of temporary water bodies is limited (Williams 2006). Published studies on physicochemical aspects and the phytoplankton of temporary waters are usually limited to a single lake or system and are largely descriptive (e.g., García et al. 1997; Kelley et al. 2000; Gaberscik et al. 2003). To our knowledge, no study has yet described the seasonal dynamics of multiple temporary water bodies or reported comparisons of their trophic status and nutrient limitation with those of permanent lakes. In this study, we aim to describe month-to-month variation, trophic status, and relationships between nutrients and phytoplankton biomass in Irish seasonal lakes (turloughs) and to compare the results with studies of permanent lakes in Ireland and elsewhere.

Turloughs are depressions in karstic areas that flood seasonally, mostly by groundwater, and that support soils and ecological communities characteristic of wetlands (Working Group on Groundwater 2004). They usually start to fill between September and November and normally persist until late spring or early summer. With no natural surface outlets, they drain to groundwater, generally via swallow holes or estavella (openings through which water enters and exits at different times) (Coxon 1987*b*). Although some may retain standing water throughout the year, most drain completely. Summer use is normally as pasture land (Reynolds 1982). They rarely exceed 5 m in depth, although depths of up to 15 m have been noted (H. Pereira, personal observation, and O. Naughton, Department of Civil, Structural and Environmental Engineering, Trinity College Dublin, Ireland, personal communication, 2009). These ecosystems are virtually unique to Ireland (Goodwillie 2001; Sheehy Skeffington et al. 2006), occurring predominantly in the west of the coun-

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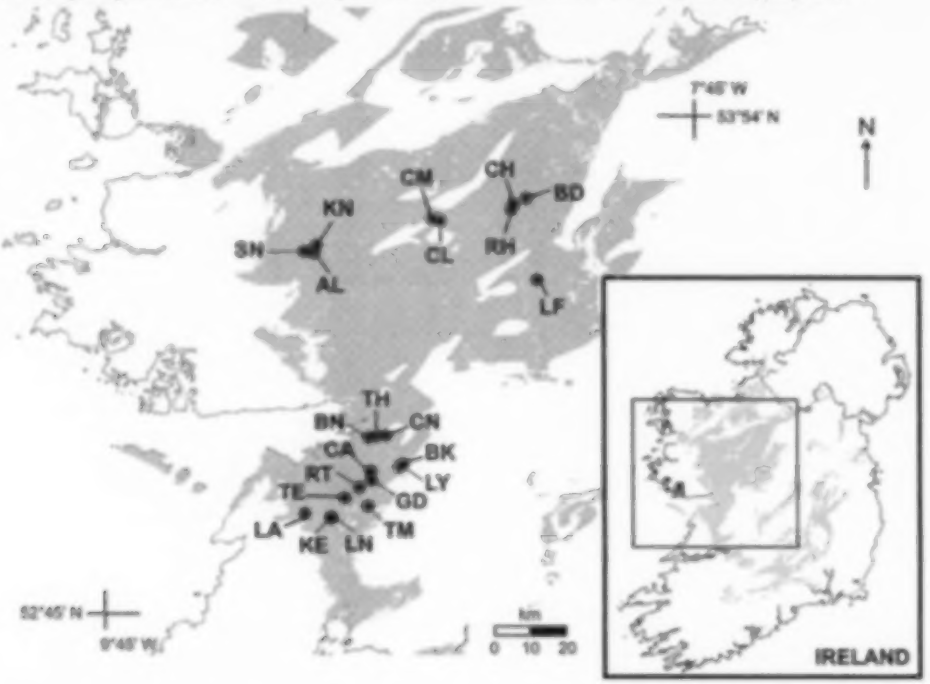
Fig. 1. Geographical distribution of the 22 turloughs studied (abbreviations are explained in Table 1). Shaded areas correspond to areas of pure bedded limestone (geological data from the Geological Survey of Ireland database: www.gsi.ie/Mapping.htm).



try where the dominant bedrock is pure bedded carboniferous limestone covered with thin and permeable glacial drift (Coxon 1987*a*). Turloughs are threatened by artificial drainage, eutrophication, and management changes (Sheehy Skeffington et al. 2006), and a number of them are protected under the European Union (EU) Habitats Directive (EU 1992) and the Birds Directive (EU 1979). Additionally, turloughs are protected and have been defined as Groundwater Dependent Terrestrial Ecosystems under the Water Framework Directive (EU 2000; Working Group on Groundwater 2004).

At present, there are no published comprehensive data on the algae and chemical characteristics of turlough waters (Working Group on Groundwater 2004). Accordingly, their trophic status has never been determined directly, though values of "trophic sensitivities" have been estimated, based on the proportion of enrichment-sensitive terrestrial plant communities present in the basins (Goodwillie 1992; Working Group on Groundwater 2004). Potential sources of nutrients to turloughs include the catchments and the soils within the basins. Intimate surface water – groundwater relationships and high underground flow rates of karstic hydrological systems render turloughs quite vulnerable to anthropogenic pressures (Coxon and Drew 1998; Johnston and Peach 1998; Tynan et al. 2005), particularly to nutrient loading (Kilroy et al. 2001; Kilroy and Coxon 2005). Catchment areas of turloughs are largely dominated by agricultural land, and agricultural activities within catchments are expected to be major contributors of nutrients to turlough waters. There is also the possibility of release of nutrients from the soil to the water following inundation, as turlough soils are usually covered with lush grassland that is often used for grazing during the dry months.

Phosphorus (P) is generally the most important limiting nutrient for algal production in temperate lakes (e.g., Hutchinson 1973; Reynolds 1984; Correll 1998). Consequently, many studies of lakes have found P to be positively correlated with algal biomass (Sakamoto 1966; Dillon and Rigler 1974; Phillips et al. 2008), whereas others have found nitrogen (N) to be an important limiting nutrient (e.g., Kanninen et al. 1982; Canfield 1983). Some studies showed that P and N colimitation can occur (e.g., Elser et al. 2007) and that these nutrients can also be alternating or colimiting in time within the same lake (Kanninen et al. 1982; Morris and Lewis 1988; Sterner 1994). Additionally, the ratio of total nitrogen (TN) to total phosphorus (TP) (TN:TP) has been shown to influence algal biomass (McCauley et al. 1989), but it is normally found that N has a more pronounced limiting role only when TN:TP is low, usually below 17 (Sakamoto 1966; Smith 1982; Phillips et al. 2008). The importance of the availability of dissolved nutrients in the water (i.e., the fraction available for algal uptake), rather than the totals, has also been noted (Pearsall 1932; Reynolds 2006), and this has been acknowledged in experimental and field studies (e.g., Sterner 1994). It has been proposed that phytoplankton growth will not be limited by P when soluble reactive phosphorus (SRP) concentrations exceed 10 $\mu g \cdot L^{-1}$ (Organisation for Economic Co-operation and Development (OECD) 1982; Sas 1989).

Given that turloughs are ephemeral water bodies that occur mostly when day length (photoperiod) and temperature (factors that are known to limit phytoplankton growth (Rey-

Table 1. Turlough locations, areas, and durations of flooding.

Turlough	Irish national grid	Area (ha) (Goodwillie 1992)	No. of months flooded 2006–2007
Ardkill (AL)	M27360 62500	16.0	9
Ballinderreen (BN)	M41060 14920	47.2	8
Blackrock (BK)	M49780 08130	40.3	6
Brierfield (BD)	M81600 76560	52.9	9
Caherglassaun (CN)	M41550 06340	41.8	9
Caranavoodaun (CN)	M45450 15450	24.8	8
Carrowreagh (CH)	M78420 75080	26.3	7
Coolcam (CM)	M57420 71390	67.1	9
Croaghill (CL)	M59631 70711	37.4	9
Garryland (GD)	M41750 04050	20.4	7
Kilglassaun (KN)	M27860 64550	49.9	8
Knockaunroe (KE)	R31400 94180	42.5	8
Lisduff (LF)	M84250 55500	54.1	8
Lough Aleenaun (LA)	R24740 95440	10.7	7
Lough Coy (LY)	M49000 07500	—	7
Lough Gealain (LN)	R31450 94730	—	8
Rathnalulleagh (RH)	M77710 73760	26.4	7
Roo West (RT)	M38630 02210	—	8
Skealoghan (SN)	M24750 62900	28.0	7
Termon (TN)	R40920 97350	38.2	9
Tullynafrankagh (TH)	M43210 15340	—	9
Turloughmore (TE)	R34950 99480	21.7	5

nolds 2006)) are at an annual minimum, it was expected that these systems would have low algal production through much of the flooding season. Furthermore, the rapidly fluctuating water levels (Moran et al. 2008) and presumed relatively low water residence times could pose further constraints on algal biomass in turloughs besides nutrient levels, as has been shown for lakes (Na and Park 2006; Elliott et al. 2009).

Materials and methods

Site selection

Twenty-two turloughs were chosen to represent a broad geohydrological spectrum (Fig. 1). Existing preliminary data on trophic sensitivity of the turlough vegetation communities and initial indications of geohydrological settings of a large number of turloughs were used for selection. The geographical coordinates, surface area, and the number of months flooded during the sampling period (October 2006 to June 2007) are provided for each turlough (Table 1). All sites are designated as candidate Special Areas of Conservation (cSAC) under the Habitats Directive (EU 1992), except for Brierfield, Carrowreagh, and Rathnalulleagh.

Water sampling and analysis

Samples were collected by throwing a weighted 5 L plastic bottle, attached to a rope, from the shore to an area of open water. Locations near springs and swallow holes were avoided. Samples were collected during the second week of each month.

Samples were analysed for TP, TN, SRP, total oxidized nitrogen (TON), chlorophyll *a* (Chl *a*), alkalinity, and colour following standard methods (Clesceri et al. 1989). TP concentration was obtained by acidic persulphate digestion of samples at 120 °C and subsequent determination of phosphate by colorimetry (Eisenreich et al. 1975; Shimadzu UV-1601 spectrophotometer). SRP was measured in filtered samples (Whatman GF/C filter) by the colorimetry method used for TP but without digestion. TN was measured after alkaline persulphate digestion of samples at 120 °C followed by measuring the resulting nitrate by automated colorimetry (Grasshoff et al. 1999; Bran+Luebbe AutoAnalyzer 3). TON was measured on filtered samples using ion chromatography (Dionex Instruments ICS-1500). Chlorophyll *a* was determined by methanol extraction of Whatman GF/C filters, followed by absorbance measurement of the extract at 665 nm (Chl *a* peak) and 750 nm (turbidity correction; Standing Committee of Analysts 1980; Shimadzu UV-1601 spectrophotometer). Replicates (at least two from each original 2.5 L sample) were used in the analyses, except in the analyses of alkalinity and Chl *a* for which separate repeatability experiments were carried out.

Data analyses

All statistical analyses were carried out using SPSS 16.0 for Windows (Field 2005). TP, TN, and Chl *a* concentrations were log-transformed for the purpose of testing regressions, to assure normality of the distribution, and to allow comparisons with regression results in the literature. Normality of distributions was tested by applying the Kolmogorov–Smirnov test, and all data used in regressions were found to be normally distributed. TP and TN were tested as predictors of Chl *a* concentrations using a linear regression model, both using all monthly values and flooding-season averages. A significant regression relationship between TP and Chl *a* found for turloughs was compared with similar relationships from the literature on permanent lakes. We assessed whether there were statistical

Table 2. Mean values, standard deviations (SD), and ranges for total phosphorus (TP), soluble reactive phosphorus (SRP), total nitrogen flooding season; also shown are trophic status classification based on OECD (1982).

	TP ($\mu g \cdot L^{-1}$)		SRP ($\mu g \cdot L^{-1}$)		TN ($mg \cdot L^{-1}$)		TON ($mg \cdot L^{-1}$)	
Turlough	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range
Ardkill	82±33	32.3–117.1	42±27	1.6–82.6	1.74±1.04	0.6–3.8	1.25±1.04	0–3.1
Ballinderreen	12±9	4.6–27.8	1±0.4	0.3–1.6	0.73±0.41	0.2–1.5	0.15±0.21	0–0.5
Blackrock	52±16	27.4–73.5	27±10	15.1–38.0	1.72±0.29	1.3–2.1	1.21±0.37	1.0–2.0
Brierfield	20±10	12.1–41.2	2±1	0.5–3.3	0.57±0.15	0.4–0.8	0.06±0.11	0–0.3
Caherglassaun	43±12	31.8–66.7	19±7	6.7–29.8	1.22±0.23	0.9–1.6	0.85±0.52	0.3–0.9
Caranavoodaun	11±4	6.3–18.6	2±1	0.8–3.1	2.30±1.42	0.8–5.1	1.86±1.42	0–4.1
Carrowreagh	43±8	32.8–55.7	8±8	1.8–21.6	0.91±0.45	0.5–1.6	0.36±0.41	0–1.0
Coolcam	34±21	8.8–80.8	4±4	0.3–13.9	1.27±0.67	0.5–2.6	0.92±0.59	0–1.7
Croaghill	25±17	10.5–65.0	4±2	1.9–8.1	1.17±0.68	0.4–2.3	0.71±0.67	0–1.7
Garryland	25±7	11.7–31.4	11±4	3.5–14.3	1.08±0.42	0.6–1.8	0.57±0.22	0.3–0.8
Kilglassan	27±12	13.9–44.6	5±4	1.6–12.1	1.45±1.04	0.2–3.3	1.07±1.00	0–2.7
Knockaunroe	4±2	1.4–7.1	1±0.4	0–1.3	0.55±0.15	0.3–0.8	0.30±0.15	0–0.4
Lisduff	7±2	4.2–9.6	2±1	0.9–2.4	1.90±0.77	0.7–3.1	1.75±0.84	0–2.5
Lough Aleenaun	31±14	17.0–59.9	9±6	0.7–16.6	1.25±0.27	0.8–1.5	1.01±0.28	0.7–1.4
Lough Coy	43±16	24.7–61.9	21±10	4.8–34.4	1.41±0.26	1.1–1.9	1.00±0.25	0.6–1.3
Lough Gealain	4±1	1.7–5.5	1±0.4	0.2–1.3	0.59±0.20	0.3–0.9	0.35±0.12	0.1–0.5
Rathnalulleagh	45±22	18.9–83.9	3±2	1.0–6.5	1.25±0.46	0.7–1.9	0.66±0.49	0–1.4
Roo West	10±4	4.5–17.7	1±1	0.2–1.6	0.59±0.29	0.2–1.0	0.25±0.24	0–0.6
Skealoghan	20±6	12.7–27.2	6±6	1.2–17.7	0.92±0.69	0.4–2.2	0.50±0.65	0–1.8
Termon Lough	15±8	4.3–30.2	2±1	1.5–5.1	0.62±0.34	0.4–1.2	0.28±0.32	0–0.8
Tullynafrankagh	33±18	14.7–58.9	3±2	1.6–7.2	2.14±1.24	0.9–4.6	1.49±1.33	0–3.8
Turloughmore	19±11	10.2–35.7	3±2	1.6–5.4	0.63±0.43	0.2–1.3	0.33±0.37	0–0.8

[a]Fixed boundary system used.

differences in slope and intercept between the model for turloughs and those for permanent lakes using a *t* test (Field 2005).

Algal biomass in temperate permanent lakes is often assumed to be higher in summer than in winter (e.g., Dillon and Rigler 1974; Phillips et al. 2008). Although this question has already been addressed for a number of lakes (Marshall and Peters 1989), statistical evidence on whether algal biomass in summer is in fact higher than in winter in Irish lakes is desirable. For that, we analysed long-term Chl *a* data for Lough Leane and Muckross, two hydrologically connected lakes in Killarney, Ireland. Lough Leane is a mesotrophic lake considered to be human-impacted (Champ 1998; Clabby et al. 2008), and Muckross is oligotrophic and nonimpacted (Free et al. 2006). Averages of Chl *a* over 34 years (for Lough Leane) and 23 years (for Muckross) were calculated for two periods: (*i*) October to May inclusive ("winter", when most of the turloughs were full) and (*ii*) June and September inclusive ("summer"). Paired *t* tests were used to test for differences between summer and winter Chl *a* in the two lakes.

Results

Ranges of values of nutrients and Chl *a* in turloughs

Turloughs varied considerably in the measured levels of nutrients and Chl *a* (Table 2). Average TP ranged between 4.0 and 82.1 $\mu g \cdot L^{-1}$, with 16 sites having a mean TP value <35 $\mu g \cdot L^{-1}$ and three sites having <10 $\mu g \cdot L^{-1}$ (standard deviation (SD) of averages across turloughs = 18.7 $\mu g \cdot L^{-1}$); average TN ranged from 0.5 to 2.3 $mg \cdot L^{-1}$ (SD = 0.5 $mg \cdot L^{-1}$) and average Chl *a* ranged from 1.1 to 18.4 $\mu g \cdot L^{-1}$ in all turloughs except in Rathnalulleagh, which had a seasonal average of 33.5 $\mu g \cdot L^{-1}$ (SD of averages across turloughs = 7.8 $\mu g \cdot L^{-1}$). The high Chl *a* average in Rathnalulleagh is owing to high values during the season (between 6 and 48 $\mu g \cdot L^{-1}$) but also to an extreme value in October (110.5 $\mu g \cdot L^{-1}$). Average TN:TP were above 21 for all turloughs (Table 2). Monthly values below 17 occurred in only seven turloughs, usually in only one or two months at the beginning or end of the season, when TN was low.

Average SRP was <5 $\mu g \cdot L^{-1}$ in 14 turloughs and <10 $\mu g \cdot L^{-1}$ in 17 turloughs. Garryland, Caherglassaun, Lough Coy, Blackrock, and Ardkill were turloughs that showed SRP seasonal averages >10 $\mu g \cdot L^{-1}$ (Table 2). SRP was 17.9% of TP on average for all turloughs (SD = 7.3%, $N = 17$) except the latter five named above, for which SRP was 46.7% of TP on average (SD = 6.6%, $N = 5$). TON was very low (<0.15 $mg \cdot L^{-1}$ on average) in two turloughs (Brierfield and Ballinderreen). Average TON was <0.5 $mg \cdot L^{-1}$ in nine turloughs and <1.0 $mg \cdot L^{-1}$ in 16 and the highest average was 1.86 $mg \cdot L^{-1}$ in Caranavoodaun. The percentage TON of TN for all turloughs (except Ballindereen and Brierfield, both below 15%) was 55.6% (SD = 15.9%, $N = 20$), with the highest value in Lisduff (85.4%).

Month-to-month variation of nutrients and Chl *a*

TN concentrations showed a clear seasonal pattern in all turloughs, which was defined by an increase until December or January followed by a steady decline (Fig. 2). However, TP and Chl *a* did not show any seasonal pattern that was common to all turloughs (Fig. 2). TP was often high in the

(TN), total oxidized nitrogen (TON), chlorophyll *a* (Chl *a*), and mean values for alkalinity and colour in the studied

Chl *a* ($\mu g \cdot L^{-1}$)					OECD trophic status [a] based on	
Mean ± SD	Range	TN:TP	Alkalinity ($mg \cdot L^{-1}$ $CaCo_3$)	Colour ($mg \cdot L^{-1}$ PtCo)	Mean TP	Mean Chl *a*
12.7±16.1	1.8–52.4	26	220	28	Eutrophic	Eutrophic
3.0±2.7	1.0–8.8	73	184	17	Mesotrophic	Mesotrophic
1.3±0.7	0.7–2.5	35	167	72	Eutrophic	Oligotrophic
5.0±3.1	1.1–9.9	32	210	36	Mesotrophic	Mesotrophic
3.3±4.3	0.8–13.5	30	112	85	Eutrophic	Mesotrophic
2.8±2.8	0.7–9.2	258	217	25	Mesotrophic	Mesotrophic
12.1±9.5	2.8–31.3	21	219	48	Eutrophic	Eutrophic
18.1±11.6	3.0–31.7	45	214	23	Mesotrophic	Eutrophic
7.6±10.3	1.4–32.0	57	220	44	Mesotrophic	Mesotrophic
1.1±0.6	0.4–2.0	46	122	80	Mesotrophic	Oligotrophic
5.0±3.4	1.6–10.6	58	216	28	Mesotrophic	Mesotrophic
1.2±0.7	0.5–2.2	147	139	10	Oligotrophic	Oligotrophic
1.4±0.5	0.8–2.1	282	228	21	Oligotrophic	Oligotrophic
9.2±12.8	1.5–36.6	48	160	14	Mesotrophic	Eutrophic
5.2±5.6	0.7–13.5	36	143	72	Eutrophic	Mesotrophic
1.1±0.7	0.3–2.6	163	135	8	Oligotrophic	Oligotrophic
33.5±36.5	6.3–110.5	34	236	28	Eutrophic	Hypertrophic
2.1±1.1	0.7–3.7	65	141	14	Oligotrophic	Oligotrophic
6.9±4.2	1.5–11.8	37	198	26	Mesotrophic	Mesotrophic
3.1±2.4	0.6–8.1	49	226	21	Mesotrophic	Mesotrophic
18.4±20.0	3.0–69.4	93	234	36	Mesotrophic	Eutrophic
4.8±4.6	0.6–11.3	46	168	11	Mesotrophic	Mesotrophic

winter months but not always and not exclusively (see e.g., Rathnalulleagh, Ardkill, and Brierfield in Fig. 3). Chlorophyll *a* peak values were usually multiples of those at other times (for examples, see Fig. 3). Chlorophyll *a* was highest in the period between November and February inclusive in 14 turloughs (five in both November and February, four in January). Three turloughs had peak Chl *a* in October, one in March, one in April, and three in May. Values as high as 13.5 $\mu g \cdot L^{-1}$ in Lough Coy, 14.5 $\mu g \cdot L^{-1}$ in Carrowreagh, 22.4 $\mu g \cdot L^{-1}$ in Coolcam, 24.0 $\mu g \cdot L^{-1}$ in Rathnalulleagh, and even 69.4 $\mu g \cdot L^{-1}$ in Tullynafrankagh were found in the middle of winter (January). Values of Chl *a* ≥10 $\mu g \cdot L^{-1}$ on the first sampling date were found in seven out of the 22 turloughs (Ardkill, Carrowreagh, Coolcam, Lough Aleenaun, Rathnalulleagh, Skealoughan, and Tullynafrankagh). A striking example was that of Rathnalulleagh, with a peak of 110.5 $\mu g \cdot L^{-1}$ of Chl *a* in October (Fig. 3). In relation to the issue of seasonal differences of Chl *a* in permanent lakes, our analyses of summer and winter Chl *a* in the Killarney lakes showed that Chl *a* was significantly higher in summer than in winter ($p < 0.001$), both in Lough Leane (9.1 $\mu g \cdot L^{-1}$ vs. 3.3 $\mu g \cdot L^{-1}$, respectively) and in Muckross (2.6 $\mu g \cdot L^{-1}$ vs. 1.4 $\mu g \cdot L^{-1}$, respectively). The relevance of this to the trophic status comparison between turloughs and lakes is discussed below.

Relationships between nutrients and Chl *a*

Chlorophyll *a* was not significantly correlated with TN (log of monthly values and seasonal averages, $N = 22$, $p > 0.30$). However, the linear regression between TP and Chl *a* was significant, using both all monthly values ($\log \text{Chl } a = 0.754 \log \text{TP} - 0.449$, $R^2 = 0.317$, $p < 0.001$, $N = 169$) and seasonal averages ($\log \text{Chl } a = 0.663 \log \text{TP} - 0.345$, $R^2 = 0.342$, $p = 0.004$, $N = 22$). If the five turloughs with average SRP values >10 $\mu g \cdot L^{-1}$ (Ardkill, Blackrock, Lough Coy, Caherglassaun, and Garryland) are omitted from this analysis, the regression shows a considerably better fit ($\log \text{Chl } a = 1.147 \log \text{TP} - 0.802$, $R^2 = 0.844$, $R = 0.919$, $p < 0.001$, $N = 17$; Fig. 4). The plot of average Chl *a* against average TP and the regression line including all turloughs except the five mentioned is depicted (Fig. 4). We compared this with three equivalent lines found for permanent lakes in the literature: a study of TP – Chl *a* regression using data for summer Chl *a* and spring TP in lakes in North America (eq. 2 in Dillon and Rigler 1974); a regression between TP and Chl *a* using reported mean annual values for 15 Irish lakes (table 2 in Champ 1998); and a study of the TP – Chl *a* relationships during the growing season (April–September) of high alkalinity (>50 $mg \cdot L^{-1}$ $CaCO_3$), shallow (3–15 m), and very shallow (<3 m) European lakes that are comparable with turloughs (eq. 6 in Phillips et al. 2008). Statistical analysis revealed that there were no significant differences between the turloughs and Champ's (1998) model ($t_{[30]} = 0.12$ for the slope and $t_{[30]} = 0.80$ for the intercept, $p > 0.05$). The Phillips et al. (2008) model had the same slope ($t_{[178]} = 1.92$, $p > 0.05$) but a significantly higher intercept ($t_{[178]} = 2.67$, $p < 0.05$) than the turlough model, and Dillon and Rigler's (1974) model had the same intercept ($t_{[61]} = 1.80$, $p > 0.05$) but a marginally significantly higher slope ($t_{[61]} = 2.03$, $p < 0.05$). When an outlier in the Dillon and Rigler's (1974) data set (TP = 180 $\mu g \cdot L^{-1}$ and Chl *a* = 260 $\mu g \cdot L^{-1}$, far above the

range in turloughs) is removed from the regression analysis, the new model becomes statistically similar to the turlough model (t_{slope} = 1.79 and t_{inter} = 1.57 for the slope and intercept, respectively, $p > 0.05$). Furthermore, by comparing the turlough regression model with a wide range of lake models, it was found that the predictor values of Chl *a* from our model were within the range of the predictor values obtained from lake models (Table 3, adapted from Phillips et al. 2008).

The inspection of the month-to-month variation of dissolved nutrients in relation to their total concentrations and to that of Chl *a* revealed that SRP was mostly low throughout the season in all turloughs except in the five mentioned above (with average SRP > 10 $\mu g \cdot L^{-1}$), whereas Chl *a* closely followed TP in most cases (for examples, see Fig. 3). By contrast, TON was low in relation to TN only in Ballindereen and Brierfield (Fig. 3).

Trophic status comparison with permanent lakes

We compared nutrient and Chl *a* concentrations obtained in turloughs with those of Irish lakes (Table 4). Despite the fact that turloughs are seasonal phenomena, a comparison with annual lakes is considered relevant because it permits a definition of the trophic status of turloughs in relation to lakes. Ranges of nutrient and Chl *a* concentrations were compared with five studies: a limnological study of six western lakes located in the same region as some of the turloughs studied (Allott 1990); a review of a 25-year monitoring programme on eight of Ireland's primary trout fishing lakes and comparable water bodies (Champ 1998); a detailed 3-year monitoring study of Lough Carra, an oligotrophic clear-water lake in the west of Ireland (King and Champ 2000); a comprehensive 2-year study of 31 Irish lakes (Irvine et al. 2001; Free 2002); and monitoring data for Lough Leane and Muckross in Killarney over more than 23 years. It can be seen that values for turloughs are within the range of reported values for Irish permanent lakes (Table 4). Furthermore, the ranges of TP and Chl *a* in the non-Irish lake studies of Dillon and Rigler (1974) and Phillips et al. (2008) (the linear regression models of which were compared with the one for turloughs in the present study) are similar to those found in turloughs (data inferred from graphs in these articles). By applying the OECD (1982) lake trophic classification to turloughs, it can be seen that turloughs had a wide range of trophic status (two eutrophic, eight mesotrophic, four oligotrophic, and eight with an ambiguous classification; Table 2).

Discussion

Phytoplankton biomass in turloughs and variations over time

The fact that turloughs exist as water bodies mainly in the winter could imply that these are unproductive water bodies. However, our study indicates that phytoplankton biomass as Chl *a* in turloughs was not significantly lower than that found in permanent lakes.

Chlorophyll *a* peaks in winter are not unknown in Irish lakes (Irvine et al. 2001) and elsewhere (Campos et al. 1988) but are not the norm. Although there is not a "typical" universal succession of algal biomass over time in

Fig. 2. Box plots of (*a*) total nitrogen (TN), (*b*) total phosphorus (TP), and (*c*) chlorophyll *a* (Chl *a*) through time for the 22 turloughs studied. Each shaded box represents the range in which 50% of scores fall and includes the median (horizontal bar), the top line represents the higher 25% of scores with the maximum value on top, and the bottom line represents the lower 25% of values with the minimum value on the bottom. Asterisks and circles correspond to extreme or outlier values, respectively.

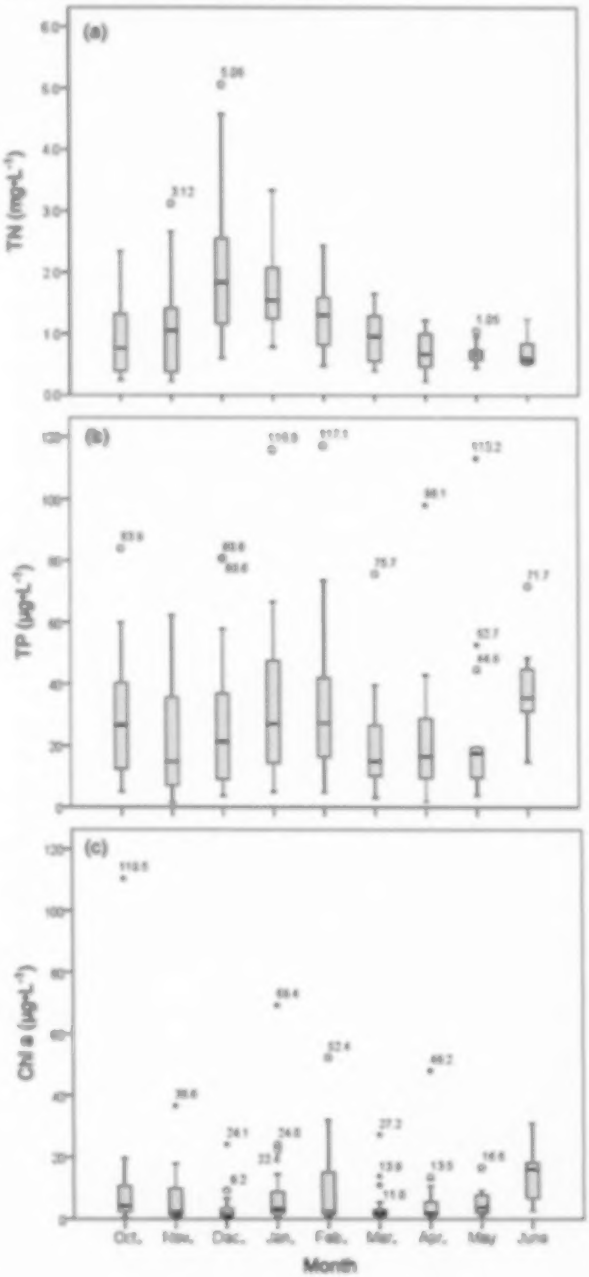
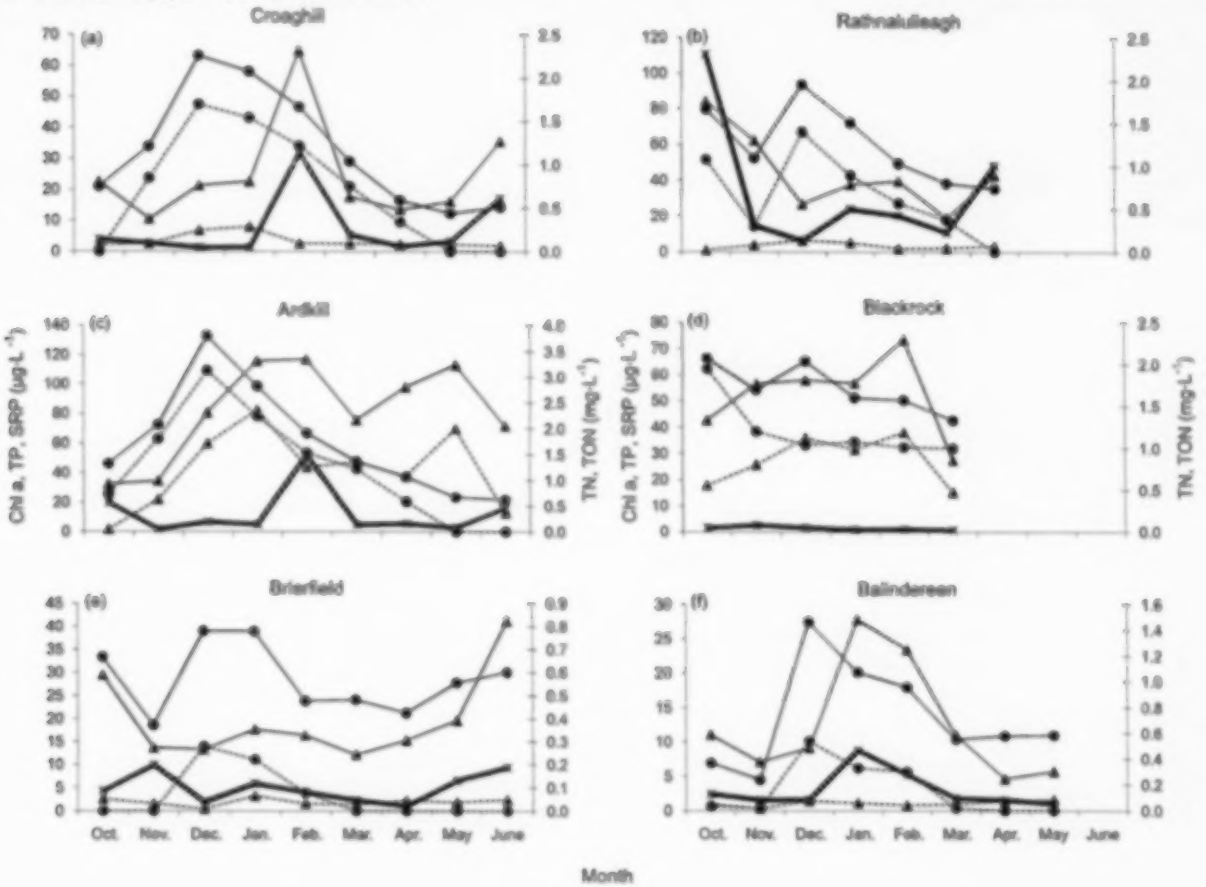


Fig. 3. Seasonal variation in some turloughs to show differences in nutrient limitation of algal biomass, suggesting (*a*, *b*) P limitation, (*c*, *d*) neither P nor N limitation apparent, and (*e*, *f*) potential P and N limitation. Legend: total phosphorus (TP; ▲ and continuous lines), soluble reactive phosphorus (SRP; ▲ and dotted lines), total nitrogen (TN) (● and continuous lines), total oxidized nitrogen (TON; ● and dotted lines), and chlorophyll *a* (Chl *a*; ° and bold lines).



lakes (Hutchinson 1967; Reynolds 1984, 2006), it is usual that algal biomass peaks in late spring or summer and is low during winter (Wetzel 2001; for Irish lakes, see Allott 1990, King and Champ 2000, and Irvine et al. 2001). Accordingly, Irvine et al. (2001) found that only two out of 31 Irish lakes in a 2-year study had a maximum concentration of Chl *a* in winter (11.7 and 22.5 µg·L^{-1}). Allott (1990), in his 2-year study of six Irish western lakes, found that Chl *a* peaked in late summer and was low throughout the winter. Our analysis of long-term data for Lough Leane and Muckross adds evidence that Chl *a* is consistently and significantly higher in summer than in winter in Irish lakes. It is worth noting here that even the summer values of Chl *a* in Lough Leane (9.1 µg·L^{-1}, on average, over 34 years with an absolute maximum of 118.9 µg·L^{-1}) are within the range of values obtained in the turloughs studied. Thus, it is notable to conclude that turloughs can reach the same, or higher, levels of Chl *a* in winter as those reached in mesotrophic lakes in the summer alone. A factor contributing to high production may be that turloughs are, in general, shallow lakes with nonturbid waters (turbidity values were below 5.5 NTU as a seasonal average for all turloughs, data not shown). This may result in better illumination in the euphotic zone (Scheffer 1998; Nõges and Nõges 1999; Nõges et al. 2003). Clearly, more research is needed to help identify the factors responsible for the high yields of phytoplankton biomass in turloughs.

In relation to Chl *a* variation over time, it was initially hypothesized that abundance would be low in the beginning of flooding and throughout the winter months and, as the days became longer and warmer, that the abundance of algae in the water would increase. In "mesotrophic" shallow temperate lakes for example (the ones closest to resembling turloughs from the different "types" described in the literature), the "typical" succession is considered to be that of a diacmic pattern, with peaks in late spring (April–May) and late summer (August) (Hutchinson 1967; Reynolds 1984). In turloughs, there was not a common pattern of Chl *a* variation over time, and peak Chl *a* occurred at very different times during the season across turloughs. Nevertheless, the majority of turloughs had their maxima in November, January, and February, which is typically the darkest

Fig. 4. Relationship between average log total phosphorus (TP) and average log chlorophyll *a* (Chl *a*) in the 22 turloughs studied. The continuous line represents the linear regression fit (log Chl *a* = 1.147 log TP – 0.802, R^2 = 0.844, N = 17), and broken lines represent linear regression lines for lakes in the literature. Labelled turloughs were omitted from the regression because Chl *a* concentration was not considered to be limited by TP in these turloughs.

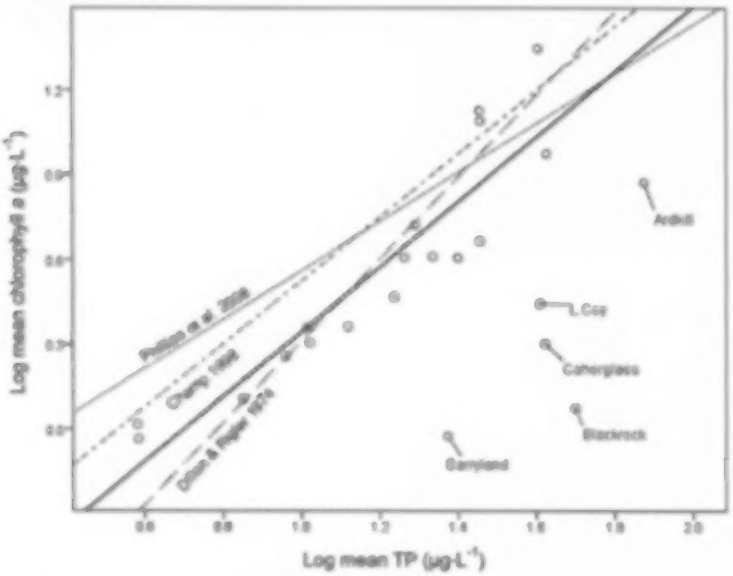


Table 3. Log TP – log chlorophyll *a* (Chl *a*) regression equations from this study (in italics) and from permanent lakes in the literature (adapted from Phillips et al. 2008); the values underlined are for the regression lines depicted in Fig. 4.

Reference	Constant	Slope	R^2	Predicted Chl *a*[a]
OECD 1982	–0.432	0.79	0.77	5.4
White 1983	–0.638	0.940	0.45	6.5
Prairie et al. 1989	–0.390	0.874	0.69	9.1
Turloughs	*–0.802*	*1.147*	*0.84*	*9.3*
Vollenweider 1976	–0.432	0.910	0.76	9.4
Nürnberg 1996	–0.250	0.799	0.64	9.6
Phillips et al. (2008) (high alkalinity shallow and very shallow lakes)[b]	–0.306	0.868	0.52	10.8
Dillon and Rigler 1974	–1.136	1.449	0.92	12.6
Phillips et al. (2008) all lakes[b]	–0.455	1.026	0.78	13.5
Champ 1998	–0.595	1.121	0.76	13.7
Jones and Bachmann 1976	–1.090	1.460		14.8
Seip et al. 2000	–0.443	1.123	0.93	19.5

[a]To facilitate comparison, values are ordered by increasing predicted chlorophyll *a* (in µg·L^{-1}) when TP = 35 µg·L^{-1}.
[b]In Phillips et al. (2008), the authors tested regressions for all lakes in the database but also for subgroups of lakes with particular hydrochemical characteristics.

and coldest time of the year. The lowest average water temperatures were recorded in February (6 °C), and temperatures were below 10 °C from November to March inclusive. García and Niell (1993) and García et al. (1997) also found that Chl *a* and phytoplankton abundance was highest in winter in a temporary saline lake in Spain, with values similar to those found in turloughs. They found that the decline of phytoplankton biomass in spring was coupled with an increase in zooplankton grazers and lower allochthonous input. The decline of phytoplankton biomass in spring in turloughs could also be due to higher grazing pressures (see also Barone and Naselli-Flores 2003) and perhaps a lower availability of nutrients during that phase; instead, phytobenthos may be dominating the autotrophic community at this stage (e.g., García and Niell 1993; Blindow et al. 2002).

Another surprising feature of turloughs is the often high value of Chl *a* found at the beginning stages of flooding. A striking example in our study was that of Rathnaluleagh in October (110.5 µg·L^{-1}), measured only about 19 days after the onset of flooding (O. Naughton, Department of Civil,

Table 4. Range of values for turloughs and a number of Irish lakes reported in the literature of average annual (flooding season in case of the turloughs) total phosphorus (TP), total nitrogen (TN), chlorophyll *a* (Chl *a*), and maximum chlorophyll *a* (max. Chl *a*) concentrations.

Reference	No. of lakes	Mean TP	Mean TN	Mean Chl *a*	Max. Chl *a*
Turloughs	22	4–52 (82)	0.6–2.3	1.1–18.4 (33.5)	2.0–110.5
Allott 1990	6	6–22 (34)	0.5–0.8	1.7–10.2	4.5–50.6
Champ 1998	10	4–20 (44)	—	1.7–8.3 (36.2)	3.5–110.8
King and Champ 2000	1 (over 21 years)	5–20 (30)	—	<5	~2.5–~27
Irvine et al. 2001; Free 2002	31	<4–91 (530)	0.2–2.1 (3.0)	1.1–35 (58.1)	2.1–184.9
Lough Leane	1 (over 23 and 34 years)[a]	11–25	—	2.7–8.4 (23.3)	4.6–118.9
Muckross	1 (over 23 years)	3–13 (22)	—	1.1–3.0	2.1–9.0

Note: Values in parenthesis are extreme values that occurred as outliers from the bulk of the data; all units are $\mu g \cdot L^{-1}$, except for TN ($mg \cdot L^{-1}$).

[a]Over 23 years of TP measurements and 34 years of Chl *a* measurements.

Structural and Environmental Engineering, Trinity College Dublin, Ireland, personal communication, 2009). This raises the question of the origin of algal inocula that initiate phytoplankton populations in turloughs. There is recorded evidence that the seven turloughs that had high Chl *a* values in the first sampling occasion have semipermanent streams flowing and sinking into them and some have damp areas that can retain water throughout the year (Coxon 1986; Goodwillie 1992; H. Pereira, personal observation). On the other hand, turloughs such as Brierfield or Croaghill, which had relatively low Chl *a* values at the onset of flooding (<4.3 $\mu g \cdot L^{-1}$), also have evidence of semipermanent sinking streams and permanent pools, respectively. Only a closer investigation of the level of water retention through the summer in each one of the 22 turloughs would help in deciding whether the level of initial biomass is correlated with water retention throughout the dry season. On the other hand, if a minimum moisture content is present during the dry phase (estimated at 50% moisture content as percentage wet weight of sediment; Evans 1958, 1959), then algal vegetative cells or resting stages can survive during those phases. The lush grassland that normally covers turlough basins and the relatively wet Irish climate could possibly provide enough humidity to enable survival of algae through the summer, even in the driest of turloughs. Some of the algae that dominated the population in October in Rathnalulleagh (such as *Tribonema* sp. or *Chlamydomonas* sp.; H. Pereira, unpublished data) are known to be able to survive desiccation (Evans 1958, 1959).

Relationships between Chl *a* and nutrient levels

The significant linear regression found between TP and Chl *a* suggests that P is limiting phytoplankton biomass in the majority of the turloughs in our study. TN-to-TP ratios were above 17 as seasonal averages in all turloughs and in the vast majority of the monthly samples, thus emphasising the role of P rather than N as the main limiting nutrient (e.g., Phillips et al. 2008). The TP – Chl *a* regression model in turloughs was similar to the Irish permanent lakes study (Champ 1998) but not completely similar to the two non-Irish studies (Dillon and Rigler 1974; Phillips et al. 2008). The intercept in Phillips et al. (2008) model was higher than in this study, but it can be argued that the slope is the most relevant parameter in these comparisons, as it measures the rate of increase of algal biomass per increase in unit TP. In this light, turloughs showed rates of increase in Chl *a* in response to increases in TP similar to those of the Irish and the two non-Irish models. Furthermore, there is considerable variation in the linear relationships between TP and Chl *a* among lake studies, and it is seen that that the regression line in the turlough model is within the range of those found for permanent lakes. It can be concluded, therefore, that production of Chl *a* per unit TP in turloughs is within the range of values found in permanent lakes in spring and summer.

Four of the five turloughs that did not show signs of P limitation owing to high SRP values (Blackrock, Caherglassaun, Lough Coy, and Garryland) are thought to share a single explanation: they are hydrologically connected by a major karst conduit system, and unlike the other 18 turloughs in our study (and the vast majority of turloughs in general), which are fed predominantly or entirely by limestone-derived waters, they have a significant input of allogenic (nonlimestone) water from sinking streams flowing off the acidic peaty soils on the Slieve Aughty Mountains (Southern Water Global 1997). The four sites had, by far, the most highly coloured waters of the 22, presumably owing to humic acids from the peaty soils in their catchments. Colour, by either suppressing light penetration (Havens 2003; Havens and Nurnberg 2004) or sequestering important ions (Jackson and Hecky 1980), may be the main inhibitor of phytoplankton development in these turloughs. Alternatively, morphohydrological factors such as greater depths (García et al. 1997; Nõges and Nõges 1999) may be contributing to lower algal yields, as these turloughs also have the highest maximum depths and the highest volume to surface area ratios (O. Naughton, Department of Civil, Structural and Environmental Engineering, Trinity College Dublin, Ireland, personal communication, 2009). Ardkill was the fifth turlough not showing signs of P limitation (high SRP throughout season) but is only a marginal outlier in the Chl *a* – TP relationship: if this turlough is included in the regression, the model is still statistically similar to those of Champ (1998) and Phillips et al. (2008). As this turlough was also among the deepest, morphometric factors may contribute to limiting phytoplankton here, although further studies are needed to assess this.

Month-to-month variation of nutrients

The pattern of N variation was so similar across turloughs as to indicate a common underlying cause. During late autumn and winter, when rainfall exceeds evapotranspiration and plants are reducing the uptake of nutrients, nitrogen can leach from soils into groundwater (Jackson 1997; Di and Cameron 2002). Similar patterns of N variation are also reported for permanent lakes in Ireland (e.g., Allott 1990; Irvine et al. 2001) and are likely to occur in any lake with a short residence time, draining from catchments with rapid nutrient transfer (Fraterrigo and Downing 2008). For example, Foy and Girvan (2004) found that most of the nitrates found in coastal lakes in Northern Ireland came from agricultural land (the same type of dominant land use in turlough catchments) and that the higher losses of nitrate from the catchment and the higher levels in the lakes occurred in winter. King and Champ (2000) also found a positive relationship between increased rainfall and increased N levels in winter for a period of 3 years in Lough Carra in Ireland. Kelley et al. (2000) studied a karst lake in the US similar to turloughs and found higher nitrate concentrations in input zones of groundwater, thus suggesting nutrient leaching from agricultural lands within the catchment. The above considerations suggest that the catchment, rather than the soil within the turlough basin, is the primary source of nutrients in turloughs.

Phosphorus, in contrast to N, fluctuated irregularly across turloughs and over time, suggesting that the mechanisms governing P concentrations in each of the basins are site-specific. A study of the spatial heterogeneity of a subset of four turloughs in a subsequent flood season showed that turlough waters are quite homogeneous spatially, and so the issue of higher heterogeneity at the chosen sampling point (edge) is not raised (H. Pereira, unpublished data). It is known that P is less available in dissolved form than N, as it easily sorbs to particulate matter and forms stable and relatively insoluble compounds with many cations such as iron, magnesium, and calcium (e.g., Otsuki and Wetzel 1972; McDowell et al. 2004). Accordingly, it has been shown that dissolved N can move conservatively in groundwater catchments, whereas dissolved P is easily and quickly retained in most hydrogeological situations (Weiskel and Howes 1992). However, there is evidence of greater P mobility in karst aquifers, which have a significant element of conduit flow. Kilroy and Coxon (2005) studied temporal variations of P in groundwater karst springs in two catchments in western Ireland and found that although P increased with rainfall in general, the degree of response varied, and the highest peaks occurred at varying times for different springs even within the same catchment. They also found that the forms of P mainly responsible for the increases were particulate and dissolved organic P, whereas SRP remained dominant and at stable levels in most cases. However, in a few instances, increases of SRP happened concomitantly with increases in TP. These results suggest that rainfall drives flushing of P through karst catchments (causing an increase in the particulate component), but the timing and the degree of the response may be influenced by local characteristics within each catchment. Such findings help explain the different patterns of P variation found across turloughs. Judging from the studies of Kilroy and Coxon (2005), it is likely that the components responsible for the increases of P in turloughs are mainly particulate and dissolved organic forms, while directly bioavailable P remains the main fraction of groundwater P even during these peak occasions. It is suggested, however, that even particulate P can, at least in part, become available for algal uptake, mainly through dynamics in the adsorption–desorption equilibrium of P in the water (Søndergaard et al. 1992; Scheffer 1998; McDowell et al. 2004).

To conclude, our results show, rather surprisingly, that turloughs are productive water bodies with levels of nutrients and algal biomass directly comparable with those of permanent lakes. The results suggest that P concentrations determine the trophic status of most turloughs and that turloughs can produce as much algal biomass per unit TP as P-limited lakes do in spring and summer.

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Testing early life connectivity using otolith chemistry and particle-tracking simulations

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Abstract: We measured the otolith chemistry of adult Scotia Sea icefish (*Chaenocephalus aceratus*), a species with a long pelagic larval phase, along the Antarctic Circumpolar Current (ACC) and compared the chemistry with simulated particle transport using a circulation model. Material laid down in otolith nuclei during early life showed (*i*) strong heterogeneity between the Antarctic Peninsula and South Georgia consistent with a population boundary, (*ii*) evidence of finer-scale heterogeneity between sampling areas on the Antarctic Peninsula, and (*iii*) similarity between the eastern and northern shelves of South Georgia, indicating a single, self-recruiting population there. Consistent with the otolith chemistry, simulations of the large-scale circulation predicted that particles released at depths of 100–300 m on the Antarctic Peninsula shelf during spring, corresponding to hatching of icefish larvae from benthic nests, are transported in the southern ACC, missing South Georgia but following trajectories along the southern Scotia Ridge instead. These results suggest that the timing of release and position of early life stages in the water column substantially influence the direction and extent of connectivity. Used in complement, the two techniques promise an innovative approach for generating and testing predictions to resolve early dispersal and connectivity of populations related to the physical circulation of oceanic systems.

Résumé : Nous avons déterminé la chimie des otolithes des adultes de la grande-gueule antarctique (*Chaenocephalus aceratus*) de la mer de Scotia, une espèce avec une longue phase larvaire pélagique, le long du courant circumpolaire antarctique (ACC), et comparé les résultats des analyses chimiques avec le transport simulé des particules à l'aide d'un modèle de circulation. Les matériaux déposés dans les noyaux des otolithes durant le début de la vie montrent (*i*) une forte hétérogénéité entre la péninsule antarctique et la Géorgie du Sud, ce qui correspond à une frontière de population, (*ii*) des indications d'une hétérogénéité à échelle plus fine entre les zones d'échantillonnage sur la péninsule antarctique et (*iii*) une similarité entre les plates-formes de l'est et du nord de la Géorgie du Sud, ce qui indique qu'il y a là une seule population qui assure son propre recrutement. En accord avec la chimie des otolithes, les simulations de la circulation à grande échelle prédisent que les particules libérées aux profondeurs de 100–300 m sur la plate-forme de la péninsule antarctique au printemps, ce qui coïncide avec l'éclosion des larves des grandes-gueules de leurs nids benthiques, sont transportées dans le ACC sud, évitant la Géorgie du Sud, mais suivant plutôt des trajectoires le long du sud de la crête de Scotia. Ces résultats indiquent que le moment de la libération et la position des premiers stades de vie dans la colonne d'eau influencent fortement le sens et l'étendue de la connectivité. Utilisées de façon complémentaire, les deux méthodologies laissent entrevoir une approche innovatrice pour élaborer et tester des prédictions dans le but de résoudre des questions de dispersion au début de la vie et de connectivité des populations reliées à la circulation physique des systèmes océaniques.

[Traduit par la Rédaction]

Introduction

Identifying dispersal during early life

In oceanic systems, dispersal in many species occurs during early life when active movement is undeveloped and the large-scale circulation can strongly influence connectivity. Advected by currents, young fish settle across an array of environments that influence population measures such as meristics, morphometrics, vital rates, and parasite loadings. As a result, spatial heterogeneity in these measures, which mixing would homogenize, can usefully indicate separation in older life stages (e.g., Ihssen et al. 1981). However, heter-

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ogenicity so generated cannot adequately address population structure, or the direction and extent of connectivity between areas, when dispersal is restricted to early life.

Even artificial tagging is of limited use because of the size of early stages and the numbers needed to tag a large enough proportion for recapture. Yet the consequences of error can be considerable. Although population persistence, in some cases, may rely substantially on closing the life cycle through local self-recruitment (e.g., Almany et al. 2007), in other cases, dispersal and movement can connect geographically distant areas, providing coherence to strategies in which life stages take advantage of different habitats (Thorrold et al. 2001). Dispersal can also underpin abundance where otherwise few fish might occur through subsidies to local self-recruitment when immigrants subsequently breed successfully (Pulliam 1988), or through vagrancy when they do not (Sinclair 1988). Measures that do not capture early dispersal therefore run the risk of missing spatial connections and sources of recruitment and mortality, which are essential in understanding the dynamics of a population and, hence, its successful management.

Otolith chemistry provides new ways of resolving movement and has been used successfully in oceanic systems (e.g., Campana et al. 1994; Rooker et al. 2008). The chemistry reflects exposure to hydrography (Campana 1999; Walther and Thorrold 2006): because fish carry the chemistry laid down during earlier exposures, the technique provides opportunities to study large-scale migration and life history movement. However, few studies to date have focused on systems or species in which dispersal is restricted to early life.

Connectivity in the Southern Ocean

In the Southern Ocean, the Antarctic Circumpolar Current (ACC) is characterized by high-speed frontal jets embedded in its eastward flow between the southern tip of South America and the Antarctic Peninsula and into the southern Atlantic Ocean (Fig. 1). Density surfaces slope upwards toward the pole, bringing warm, nutrient-rich Circumpolar Deep Water (CDW) close to the surface near the ACC's southern boundary (Orsi et al. 1995; Pollard et al. 2002). The boundary and the Southern ACC Front (SACCF), the southern-most of the fronts in the ACC, are located close to the continental slope along the western Antarctic Peninsula (Fig. 2*a*), flooding the shelf with CDW. Above the CDW, a layer of cold Winter Water (WW) persists into summer. Over the northern shelf, however, the WW layer is eroded by mixing with warmer Antarctic Surface Water above and deep water below, creating an along-shelf gradient with a cooler version of CDW occupying depths below 200 m (Smith et al. 1999).

East of the Antarctic Peninsula, water from the Weddell Sea is transported northwards along the shelf and slope by the Antarctic Coastal Current (CC) and the Antarctic Slope Front (ASF) and offshore by the Weddell Front (WF) (Fig. 2*b*). Steered by the topography, the CC and ASF flow northwest from the tip of the Peninsula to merge at the mouth of the Bransfield Strait. Trajectories of drifters indicate that the current bifurcates along the southern Scotia Ridge, with one branch flowing west along the Peninsula and the other flowing east eventually into the ACC (Thompson et al. 2009). However, drifters are also retained by a large standing eddy or returned to the southern Scotia Ridge by a strong western boundary current in the Bransfield Strait. In contrast, water transported in the Weddell Front flows around the Powell Basin to reach the South Orkney shelf. In the Bransfield Strait, cold, fresh water transported by the ASF and higher-salinity water from the CC contrast with the modified CDW on the western shelf of the Antarctic Peninsula (Capella et al. 1992) and Warm Deep Water (WDW) from the Weddell Sea on the South Orkney shelf (Gordon et al. 2001; Heywood et al. 2004).

Simulations of hydrographic circulation based on the Harvard Ocean Prediction System (HOPS) indicate transport from the western Antarctic Peninsula to South Georgia, in which young krill are advected entrained in ACC fronts (Hofmann et al. 1998; Fach and Klinck 2006) (Fig. 1). The Polar Front crosses the northern Scotia Ridge to the west of South Georgia, whereas the SACCF loops around the eastern shelf (Fig. 2*a*) before being steered northward by the Northwest Georgia Rise. As at the western Antarctic Peninsula, mixing profiles indicate that deeper water on the shelf lies between WW and CDW, facilitated by communication with oceanic water at depth (Brandon et al. 1999; Meredith et al. 2005). However, rapid shoaling of deep water in the SACCF and its proximity suggest increasing proportions of CDW from the northern to the eastern shelves and between South Georgia and the western Antarctic Peninsula.

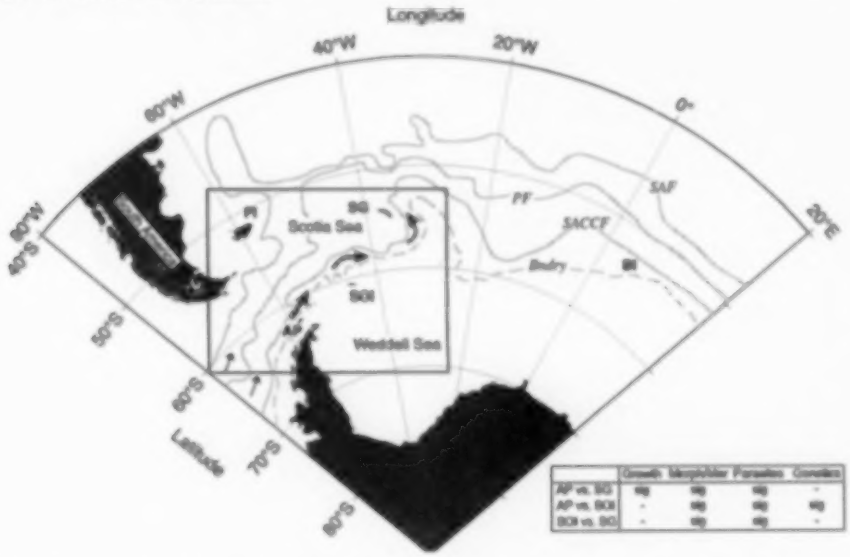
Previous studies using otolith chemistry in the Southern Ocean have successfully detected zones separated by ACC fronts (Ashford et al. 2007), known populations separated by fronts (Ashford et al. 2006; Ashford and Jones 2007), and mixing associated with transport by the ACC (Ashford et al. 2008). The technique may therefore be useful for testing putative transport pathways from the Antarctic Peninsula to South Georgia. However, these studies have compared samples taken across strong environmental gradients, often between water types, from fishing areas throughout the Southern Ocean. In contrast, discriminating chemistry from the Antarctic Peninsula and South Georgia relies on the capacity to detect different proportions of CDW between similar hydrographic regimes.

Population structure in Scotia Sea icefish

On the northern Antarctic Peninsula, extensive exploitation of fish stocks by commercial trawling ended in 1989 when the area was closed for finfishing by the Commission of the Convention for the Conservation of Antarctic Marine Living Resources (Kock 1992). Since then, the stock of Scotia Sea icefish (*Chaenocephalus aceratus*), one of the most common of the notothenioid species found there, has recovered towards original levels. However, considerable fluctuations in abundance between years may be linked to striking variation in the strength of recruiting year classes (Kock and Jones 2005).

Scotia Sea icefish are distributed on continental shelves from the northern Peninsula along the southern Scotia Ridge to South Georgia and east to Bouvet Island (Iwami and Kock 1990). Like most notothenioid species, the adults are negatively buoyant (Eastman and Sidell 2002). Evidence from growth rates (Gubsch 1980; Kompowski 1990; La Mesa et al. 2004), morphometric and meristic measurements

Fig. 1. Map of the Atlantic section of the Southern Ocean indicating the study area off the Antarctic Peninsula and South Georgia with a rectangular frame. Continuous shaded lines mark the mean position of major fronts: SAF, Sub-Antarctic Front; PF, Polar Front; SACCF, Southern Antarctic Circumpolar Current Front; Bndry, southern boundary of the ACC (shown as a broken shaded line). All fronts are after Orsi et al. (1995), with the SACCF modified after Thorpe et al. (2002). Abbreviations: FI, Falkland Islands; SG, South Georgia; SOI, South Orkney Islands; BI, Bouvet Island; AP, Antarctic Peninsula. Arrows show putative transport pathway according to Fach and Klinck (2006). Inset table summarizes population heterogeneity (sig, significant differences) in *Chaenocephalus aceratus* for the following: growth according to Gubsch (1980), Kompowski (1990), and La Mesa et al. (2004); morphometrics and meristics (morph/mer) according to Kock (1981); larval nematode infestations (parasites) according to Siegel (1980); and microsatellite frequencies (genetics) according to Papetti et al. (2009). Dashes indicate where no data are available.



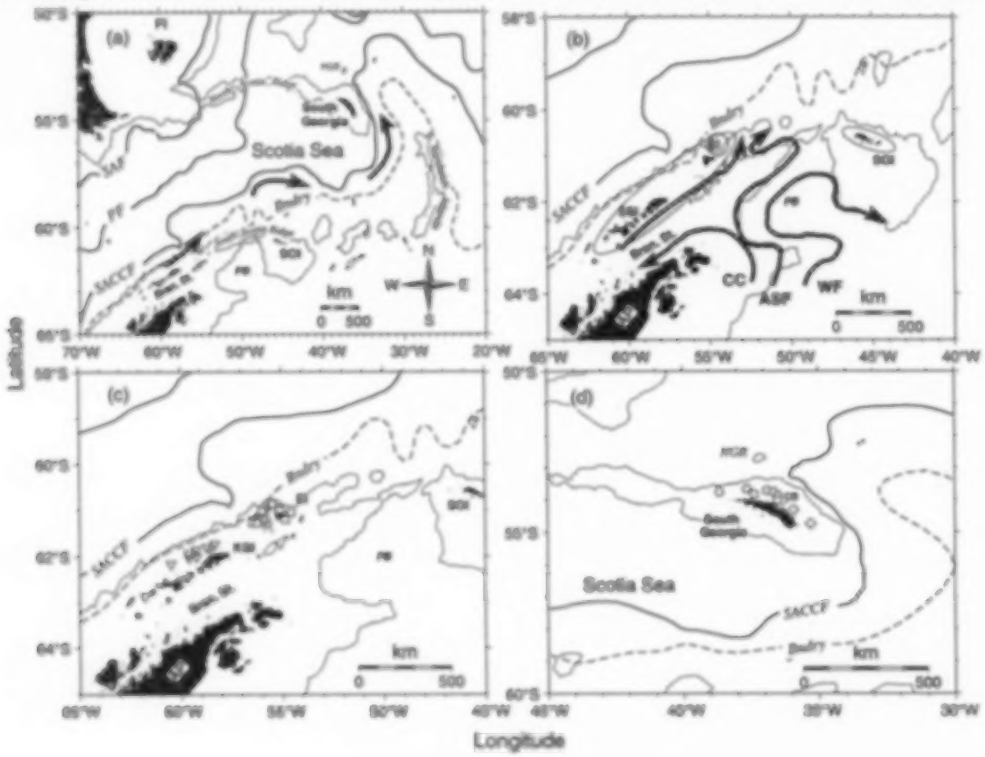
(Kock 1981), and larval nematode infestations (Siegel 1980) indicate that older stages do not mix between the Antarctic Peninsula, South Orkney Islands, and South Georgia (Fig. 1). Microsatellite data indicate population structuring, with differentiation between sampling areas at Elephant Island and the South Shetland Islands north of the Antarctic Peninsula and the South Orkney Islands (Papetti et al. 2009) (Fig. 2*b*). However, the data also showed gene flow between Elephant Island and the South Orkney Islands in both directions, considerable temporal variation, and periodic restrictions in effective population size (Papetti et al. 2007, 2009).

Spawning icefish have been found in March–April between 130 and 320 m on the shelves of the northern Antarctic Peninsula and South Georgia and also off the South Orkney Islands and Bouvet Island. Adults spawn demersally and guard eggs laid in nests in benthic depressions (Detrich et al. 2005). Along the northern Antarctic Peninsula, spawning adults are found north and west of Elephant Island and King George Island (Fig. 2*c*). The eggs hatch over a long period between July and December, peaking in November (La Mesa and Ashford 2008). The larvae are pelagic and are found in larval assemblages in the Bransfield Strait (Kellermann 1989; Loeb et al. 1993). At South Georgia, larvae occur in Cumberland Bay and over the northern shelf (e.g., North and Murray 1992; Reid et al. 2007). By contrast, large numbers of 1+-year-old icefish are found upstream on the shelf to the southwest and southeast of the island; these may later move to the northeastern shelf where the largest concentrations of adults are found (Reid et al. 2007).

The upper limit of the larval phase is as long as 400–500 days (La Mesa and Ashford 2008). Larvae are piscivorous, and as in many notothenioid species, pelagism is most likely an adaptation to optimize the availability of prey (Kellermann 1989; North and Murray 1992). This incidentally makes them vulnerable to advection, and White (1988) suggested that adults take advantage of mesoscale retaining features to spawn, thereby reducing advective mortality. For example, the larval assemblages in the Bransfield Strait may be retained in the gyre formed by westward flow of the CC and the western boundary current (Loeb et al. 1993). Eddy systems at the mouth of the Strait (Thompson et al. 2009) and over the shelves north of King George Island (Capella et al. 1992) and Cumberland Bay (Meredith et al. 2005) suggest that retention systems may structure population diversity in a similar way to that found in species outside the Antarctic (Sinclair 1988).

However, displacement by oceanic waters can dramatically alter larval assemblages on the Antarctic Peninsula (Kellermann and Kock 1988), and advective losses may account for variations in year-class strength and effective population size (La Mesa and Ashford 2008). In a system such as the ACC, where large-scale circulation is unidirectional and fish species are characterized by adults that are negatively buoyant, the resulting life history is one marked by sharp ontogenetic shifts in the spatial scales of movement, with areas potentially connected over large distances during the early life stages, but separated thereafter. Like young krill, larvae of Scotia Sea icefish displaced from these as-

Fig. 2. Detailed maps of (*a*) the study area including mean position of major fronts, with shaded arrows showing putative transport pathway according to Fach and Klinck (2006), and (*b*) schematic representation of surface circulation at the tip of the Antarctic Peninsula according to Thompson et al. (2009) and including study areas described in Papetti et al. (2009). Also shown are sampling areas for *Chaenocephalus aceratus* off (*c*) the Antarctic Peninsula and (*d*) South Georgia. Abbreviations: AP, Antarctic Peninsula; ASF, Antarctic Slope Front; Bndry, southern boundary of the ACC; Bran. St., Bransfield Strait; CB, Cumberland Bay; CC, Antarctic Coastal Current; EI, Elephant Island; FI, Falkland Islands; KGI, King George Island; NGR, Northwest Georgia Rise; PB, Powell Basin; PF, Polar Front; SACCF, Southern Antarctic Circumpolar Current Front; SAF, Sub-Antarctic Front; SOI, South Orkney Islands; SSI, South Shetland Islands; WF, Weddell Front. ASF, CC, and WF redrawn after Thompson et al. (2009). Symbols mark sampling sites at King George Island (triangles), Elephant Island (squares), South Georgia northern shelf (circles), and South Georgia eastern shelf (diamonds). Thin lines mark the 2000 m isobath.



semblages and transported along the same pathways would reach South Georgia (La Mesa and Ashford 2008) to settle as 1+-year-old juveniles on the southwestern and southeastern shelves.

To test hypotheses of local self-recruitment and early life connectivity, we measured the chemistry laid down during early life in the otolith nuclei of adult Scotia Sea icefish taken along the ACC from sampling areas on shelf regions off the northern Antarctic Peninsula and South Georgia. Local self-recruitment (e.g., Kock 2005) predicts that icefish will show heterogeneity between regions in their nucleus chemistry, but none between sampling areas within each region, reflecting exposure of larval assemblages to different environmental conditions. Alternatively, migrants displaced from larval assemblages on the Antarctic Peninsula and transported to South Georgia will show the same chemistry in their otolith nuclei as those left behind; if these migrants then mix with locally recruited fish, the nucleus chemistry of older stages will show spatial heterogeneity around South Georgia. Because homogeneity may simply reflect environmental similarity (Ashford et al. 2007), in this case, between similar regimes characterized by different proportions of CDW, we also tested for differences between sampling areas by measuring the chemistry laid down just before capture at the otolith edge. Finally, based on results from the otolith chemistry, we applied Lagrangian modelling of large-scale physical transport pathways to construct new hypotheses predicting dispersal of pelagic larvae. Output from the Ocean Circulation and Climate Advanced Modelling project (OCCAM), run by the National Oceanography Centre, Southampton, was used for the particle tracking.

Materials and methods

Otolith analysis procedures

Otoliths were collected from the continental shelf along the northern Antarctic Peninsula during a fisheries survey by the US Antarctic Marine Living Resources Program in March 2001 and around South Georgia during a similar survey by the British Antarctic Survey in September 1997. Sur-

veys consisted of a series of hauls using bottom trawls at random depth stratified station locations; full details are given in Jones et al. (2001) and Everson (1998). At each sampling site, the survey sampled fish from the catch and recorded total length, weight, sex, and maturity stages. Otoliths were collected, stored dry, and transported to Old Dominion University. To minimize ontogenetic effects, we selected adult fish >50 cm total length (TL) (Table 1) from sampling sites on the northern Antarctic Peninsula between depths of 130 and 230 m (*i*) north and west of Elephant Island and (*ii*) north and northwest of King George Island (Fig. 2*c*) and around South Georgia from sampling sites between depths of 150 and 320 m (*iii*) along the northern shelf and (*iv*) on the eastern shelf (Fig. 2*d*). For each of the four areas, 22 fish were randomly sampled from those selected and were prepared for trace element analyses.

One of each pair of sagittal otoliths was randomly selected and used for measuring concentrations of trace and minor elements. To remove any surface contamination, otoliths were rinsed in Milli-Q water, placed in 20% Ultra-Pure hydrogen peroxide for 5 min, and rinsed again in Milli-Q water. They were then ground from the anterior end using the grinding wheel of a HillQuist thin-section machine to give a transverse surface anterior of the nucleus. Otoliths were mounted on this surface using Crystalbond, which had been previously tested to ensure that it was not a source of contamination, and ground from the posterior side to reveal a transverse plane through the otolith nucleus. Near crenellations, otolith microstructure is frequently obscured (Ashford 2001) and these were avoided. The surface of the mounted thick section produced in this way was fine-ground and polished using a Crystalmaster 8 Machine with 30M and 3M Mark V Laboratory lapping film. In a clean room, the sections were rinsed in Milli-Q water under a laminar-flow hood and lapped manually using clean plastic clamps and Mark V Laboratory polishing film. Each otolith was lapped successively on three pieces of clean 3M film, finished on 0.3M film, and rinsed, and the surface was soaked with 20% Ultra-Pure hydrogen peroxide for 5 min before rinsing again. After drying, sections were removed from their slides and mounted on clean petrographic slides under a laminar-flow hood using Crystalbond. For each petrographic slide, a single section from each treatment was randomly selected and mounted in random order. The mounted sections were rinsed, sonicated for 5 min, rinsed again, all in Milli-Q water, and then left to dry.

To measure minor and trace element concentrations along the otolith edges, we used a Thermo Finnigan Element 2 double-focusing sector-field inductively coupled plasma-mass spectrometer (ICP-MS) located at the Plasma Mass Spectrometry Facility at Woods Hole Oceanographic Institution (Woods Hole, Massachusetts). Samples were introduced in automated sequence (Chen et al. 2000) using laser ablation by a New Wave Merchantek UP-213 laser ablation system and a microflow nebulizer (Elemental Scientific Inc., Omaha, Nebraska). Ablated material from the sample cell was mixed in the spray chamber with aerosol of 1% HNO_3 introduced by the nebulizer, and the mixture was then carried to the ICP torch. Blanks of 1% HNO_3 aerosol were also introduced into the chamber by the nebulizer; for quality control, we used dissolved reference material obtained from the National Resource Council of Canada. To control for operational variability in the laser ICP-MS, a randomized blocks design was used, with each petrographic slide as the blocking factor, considered randomly drawn, with each sampling area considered a fixed treatment. Blank and reference readings of count rate (counts per second) were obtained before and after random presentation of the otolith sections in each block.

Table 1. Sample size (n), total length (standard deviation, SD), and number of each sex for *Chaenocephalus aceratus* captured at sampling areas in the Scotia Sea.

Sampling area	n	Total length (cm)	Males/females
Antarctic Peninsula			
King George Island	22	56.5 (3.7)	1/21
Elephant Island	22	55.9 (4.6)	5/17
South Georgia			
Eastern Shelf	22	59.0 (4.5)	4/18
Northern Shelf	22	56.3 (4.1)	4/18

Otoliths were analysed for ^{48}Ca, ^{25}Mg, ^{55}Mn, ^{88}Sr, and ^{138}Ba and reported as ratios to ^{48}Ca. To calculate element-to-Ca ratios (Me-Ca^{-1}), background counts were subtracted from otolith counts by interpolating between readings taken before and after and at every three otoliths within each block of otoliths. The corrected otolith counts were converted to Me-Ca^{-1} concentrations using the reference readings taken immediately after each background count. To sample material laid down during early life, we placed a grid raster type 150 μm × 200 μm over the nucleus to include the primordium and material distal to the primordium, with a laser beam of diameter 20 μm, frequency at 10 Hz, and power at 60%, travelling ca. 900 μm at 6 μm·s^{-1}, and giving a predicted mean crater width of 17 μm and crater depth of approximately 100 μm (Jones and Chen 2003, eq. 3). To sample material laid down in the interval before capture, we placed a line raster type along the proximodorsal edge of the otolith and used the same settings.

Statistical methods

Because Mn-Ca^{-1} values were less than detection limits and showed no differences, they were dropped from the analyses. Two multivariate outliers were identified for the nucleus data, and four for the edge data, by plotting robust squared Mahalanobis distances of the residuals (D_i^2) against the corresponding quantiles (Q–Q plot) of the χ^2 distribution (Khattree and Naik 1999). Based on tests using Mardia's multivariate skewness and kurtosis measures ($\alpha = 0.05$) and Q–Q plots of squared Mahalanobis distances (d_i^2), neither nucleus nor edge data conformed to multivariate normality; variance–covariance matrices were not equal according to Bartlett's modification ($\alpha = 0.05$). However, univariate power transformations (e.g., Kuehl 1994, p. 121) stabilized the variances (for all element ratios, F_{max} test, $t = 4$, $\nu = 19$, $\alpha = 0.01$); the transformed data conformed to multivariate normality with equal variance–covariance matrices. The data transformations selected for the nucleus data were $y^{-0.2}$ for Mg-Ca^{-1}, $y^{0.8}$ for Sr-Ca^{-1}, and y^{-1} for Ba-Ca^{-1}. For the edge data, the data transformations were $y^{-0.2}$ for Mg-Ca^{-1}, $y^{-0.8}$ for Sr-Ca^{-1}, and $y^{0.04}$ for Ba-Ca.

Because transformed data fulfilled assumptions, we used multivariate analyses of variance (ANOVAs) to test between (*i*) population hypotheses using the nucleus data and (*ii*) environmental differences between sampling areas using the edge data. For both analyses, we constructed contrasts between (*i*) the northern Antarctic Peninsula and South Georgia, (*ii*) Elephant Island and King George Island, and (*iii*) the northern and eastern shelves of South Georgia. We used univariate models to examine the influence of each Me-Ca^{-1} ratio. We found no trend with depth. Because variance–covariance ration were equal for both nucleus and edge data, we calculated canonical discriminant variates to illustrate graphically population heterogeneity and environmental effects between areas (Khattree and Naik 2000). Because our interest did not lie in allocating samples of unknown provenance to areas or populations represented in a training set, we did not use discriminant analysis to examine classification success.

Lagrangian particle tracking

To simulate pelagic larvae transport pathways from stored OCCAM velocity fields, we used a Lagrangian particle-tracking scheme that computes translation with a first-order accurate scheme. The scheme integrates $\frac{d\vec{x}}{dt} = \vec{u}(\vec{x}, t)$, where the right-hand side is estimated through linear interpolation in time and space of stored 5-day mean three-dimensional OCCAM velocity fields. The scheme is simple and computationally efficient; the choice of a very small time step (dt = 1 min) makes it comparable with a second-order accurate scheme and ensures appropriate accuracy.

The ocean velocity fields used were taken from the OCCAM model (Webb et al. 1998; Saunders et al. 1999; Webb and de Cuevas 2003). OCCAM is a primitive equation model of the global ocean based on the Bryan–Cox ocean model. It includes a free surface and is eddy-permitting. The model output used here (run 103) has a horizontal resolution of 0.25° × 0.25° and is forced by the European Centre for Medium-Range Weather Forecasts 6 hourly wind stress data. The model has 66 depth levels and includes a sea-ice model as described by Askenov (2002). We chose the OCCAM model for this research because model output of a previous run has been shown to represent the circulation in the Scotia Sea reasonably well (Thorpe et al. 2005) and has been used in other particle-tracking studies (Ward et al. 2002; Murphy et al. 2004; Thorpe et al. 2007). In addition, the new OCCAM output has a much improved representation of the ACC fronts (Renner 2009), as well as water mass formation (Renner et al. 2009). The use of 5-day mean velocity fields means that although the model is eddy-permitting, the circulation field has reduced eddy activity compared with observations; however, the previous run of OCCAM has been shown to simulate realistic background levels of variability (Thorpe et al. 2005).

To test analytically whether icefish larvae can be transported from nesting areas at the Antarctic Peninsula to South Georgia, we simulated the trajectories of drifters released at station locations at King George Island and Elephant Island (Fig. 2*c*). Particles were released at depths between 130 and 320 m (Table 2), corresponding to those at which mature fish were taken in the interval prior to establishing nests and similar to larval depth distributions recorded by North and Murray (1992). For six different years (1995–2000), particles were released in mid-October, corresponding to the period in the year when hatching rates were highest (La Mesa and Ashford 2008), and tracked for 500 days until the end of February 1997–2002. This time span corresponds to the upper estimate of the pelagic larval phase of *C. aceratus* (La Mesa and Ashford 2008). To compare between months, particles were also released from King George Island and Elephant Island during August and September.

Table 2. Station coordinates and depths where *Chaenocephalus aceratus* were caught.

Sampling area	Latitude (°S)	Longitude (°W)	Depth (m)
EI	61.3	55.72	143
EI	61.23	55.9	137
EI	61.27	56.45	416
EI	61.15	56.12	467
EI	61.15	56.05	156
EI	61.17	55.88	112
EI	61.07	55.86	143
EI	61.02	55.98	314
EI	60.90	55.65	142
EI	60.88	55.7	173
EI	60.85	55.52	262
EI	60.87	55.48	226
EI	60.97	55.1	291
EI	61.00	55.1	132
EI	61.2	54.83	70
EI	61.28	56.22	302
EI	61.05	54.56	198
KGI	61.82	58.55	165
KGI	61.8	58.72	244
KGI	62.00	59.23	126
KGI	62.02	59.6	163
KGI	61.93	59.6	235
KGI	62.16	60.49	174
KGI	62.87	61.78	141
KGI	61.85	59.25	244
KGI	61.73	58.32	272

Note: Particles were released in OCCAM in the depth layer closest to catch depth. EI, Elephant Island; KGI, King George Island.

Results

Chemistry in the otolith nuclei showed significant differences between treatments (multivariate analysis of variance (MANOVA) Pillai's trace, F = 4.69, df = 9, $p < 0.0001$). Examining contrasts, significant differences between the northern Antarctic Peninsula and South Georgia (MANOVA Pillai's trace, F = 10.6, df = 3, $p < 0.0001$) indicated strong population structuring between regions (Fig. 3*a*). At South Georgia, fish showed no significant differences in nucleus chemistry between the northern and eastern shelves (Pillai's trace, F = 1.70, df = 3, p = 0.175), indicating no spatial structuring. These results imply little early life connectivity along the SACCF between the northern Antarctic Peninsula and South Georgia.

However, previous simulations (Fach and Klinck 2006) strongly indicated surface particle transport from the northern Antarctic Peninsula to South Georgia during austral

Fig. 3. Relationships between individual *Chaenocephalus aceratus* using canonical discriminant variates based on the chemistry of otolith (*a*) nuclei and (*b*) edges: King George Island, ▲; Elephant Island, ●; South Georgia eastern shelf, ○; South Georgia northern shelf, ×.

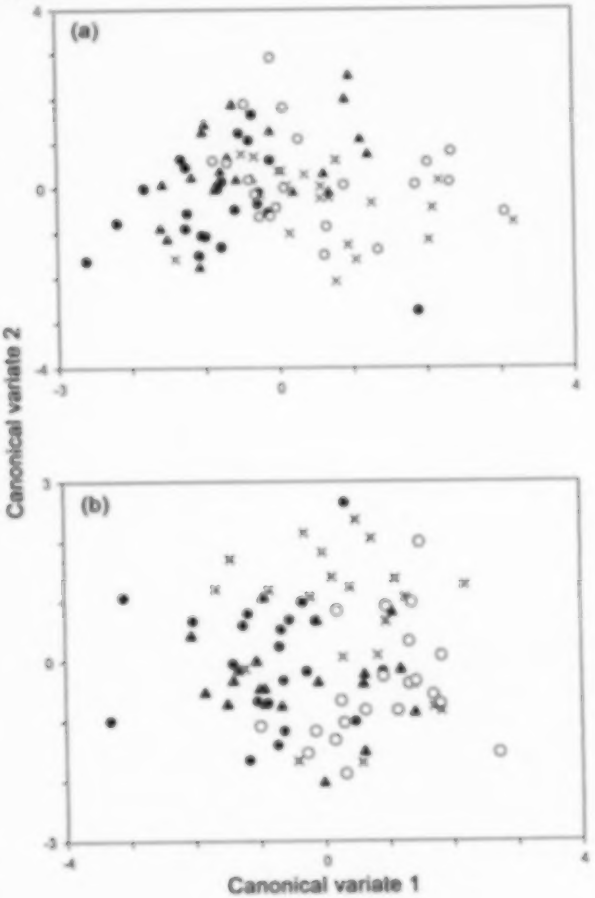
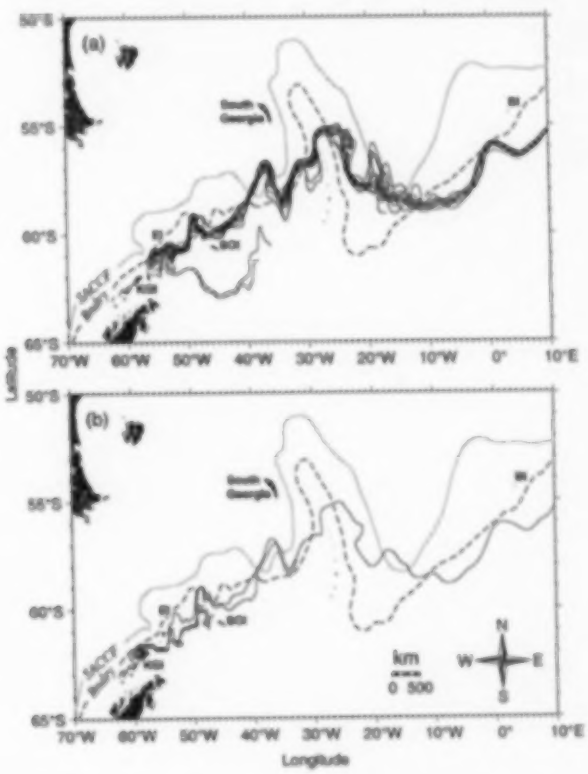


Fig. 4. Simulations of particle trajectories released at depths between 130 and 320 m from (*a*) Elephant Island and (*b*) King George Island in October 2000 and tracked for 500 days. Ocean velocity fields are from OCCAM (Webb et al. 1998; Saunders et al. 1999; Webb and de Cuevas 2003); the mode output (run 103) has a horizontal resolution of 0.25° × 0.25° and is forced by the European Centre for Medium-Range Weather Forecasts 6 hourly wind stress data. Abbreviations: BI, Bouvet Island; Bndry, southern boundary of the ACC; EI, Elephant Island; KGI, King George Island; SACCF, Southern Antarctic Circumpolar Current Front; SOI, South Orkney Islands; SSI, South Shetland Islands.



summer. Using the particle-tracking routine to examine the large-scale transport between the different regions further, we found that although the exact drifter pathways differed depending on release month and year, the outcome was consistent for all simulations: drifters released below 130 m in late winter – spring missed South Georgia entirely and instead were transported east passing South Georgia at ca. 57°S. These results are illustrated for an October 2000 release (Fig. 4). Overall, the trajectories of particles released from the Peninsula sampling areas closely followed the average position of the ACC southern boundary, passing north of the South Orkney Islands and east into the southern Atlantic through a trough north of the South Sandwich Islands. However, although particles released off Elephant Island were mostly transported along this eastward path, even reaching Bouvet Island by the end of the 500-day simulation, particles released off King George Island spent most of their transport time locally and were often advected as far east as the South Orkney Islands and rarely all the way east towards Bouvet Island. It should be noted that eddy variability not resolved in the circulation field might transport young fish in addition to the mean field. Nevertheless, these results predicted that even if larval *C. aceratus* from the two Peninsula areas are displaced and survive subsequent transport in the ACC, they are unlikely to recruit to South Georgia in the model used. Taken with the evidence from otolith chemistry, this suggests that adult fish at South Georgia come from a single, locally self-recruiting population.

In contrast, significant comparison-wise heterogeneity in nucleus chemistry between King George Island and Elephant Island (Pillai's trace, $F = 3.15$, df = 3, $p = 0.029$) suggested some population structuring on the northern Antarctic Peninsula. However, whereas the edge chemistry confirmed significant environmental differences between treatments (Pillai's trace, $F = 5.4$, df = 9, $p < 0.0001$), with significant differences between the northern and eastern shelves of South Georgia (Fig. 3*b*; Pillai's trace, $F = 5.34$, df = 3, $p =$

0.0021) and strong differences between the Antarctic Peninsula and both South Georgia sampling areas (Pillai's trace for Antarctic Peninsula vs. northern South Georgia, F = 8.03, df = 3, $p < 0.0001$; Pillai's trace for Antarctic Peninsula vs. eastern South Georgia, F = 10.75, df = 3, $p < 0.0001$). MANOVA showed no difference between King George Island and Elephant Island (Pillai's trace, F = 1.35, df = 3, p = 0.263). This suggests that the heterogeneity in nucleus chemistry on the Antarctic Peninsula was not generated by differences in environmental exposure between two locally self-recruiting populations but by an influx of fish from elsewhere.

Examining the univariate data, differences in nucleus chemistry between the Antarctic Peninsula and South Georgia were most strongly due to Mg-Ca^{-1} (Table 3*a*), consistent with powerful environmental differences indicated by the edge chemistry (Table 3*b*; Fig. 3*b*). Both nucleus and edge Mg-Ca^{-1} were similar between sampling areas at South Georgia (Fig. 5). However, significant experiment-wise differences in nucleus Mg-Ca^{-1} between Elephant Island and King George Island, despite similarity in the edge chemistry, were consistent with a putative influx of fish from elsewhere. Similarly, nucleus Ba-Ca^{-1} was strongly different between regions; edge Ba-Ca^{-1} showed strong differences between sampling areas at South Georgia, but whereas the northern shelf differentiated significantly from the Antarctic Peninsula, the eastern shelf did not. Nucleus Sr-Ca^{-1} showed no significant differences between sampling areas. However, edge Sr-Ca^{-1} showed strong differences at South Georgia, but like Ba-Ca^{-1}, the northern shelf differentiated significantly from the Antarctic Peninsula, whereas the eastern shelf did not.

Table 3. Mean square estimates from one-way analysis of variance (ANOVA) for *Chaenocephalus aceratus* using Mg-Ca^{-1}, Sr-Ca^{-1}, and Ba-Ca^{-1} sampled from otolith (*a*) nuclei and (*b*) edges.

	df	Mg-Ca^{-1}	Sr-Ca^{-1}	Ba-Ca^{-1}
(*a*) Otolith nuclei				
Sampling area	3	0.016*	945	0.031*
Residual	82	0.002	517	0.006
Contrast				
AP-SG	1	0.032*	2045	0.066*
KGI-EI	1	0.016*	37	0.002
ES-NS	1	0.001	753	0.024
(*b*) Otolith edges				
Sampling area	3	0.240*	9.9×10^{-7}*	0.0016*
Residual	80	0.021	1.8×10^{-7}	0.0004
Contrast				
AP-NS	1	0.243*	24.8×10^{-7}*	0.0029*
AP-ES	1	0.593*	0.0×10^{-7}	0.0005
KGI-EI	1	0.061	2.1×10^{-7}	0.0001
NS-ES	1	0.063	17.8×10^{-7}*	0.0044*

Note: An asterisk (*) indicates significant at experiment-wise α = 0.05. Sampling areas: KGI, King George Island; EI, Elephant Island; ES, South Georgia eastern shelf; NS, South Georgia northern shelf. df, degrees of freedom.

Discussion

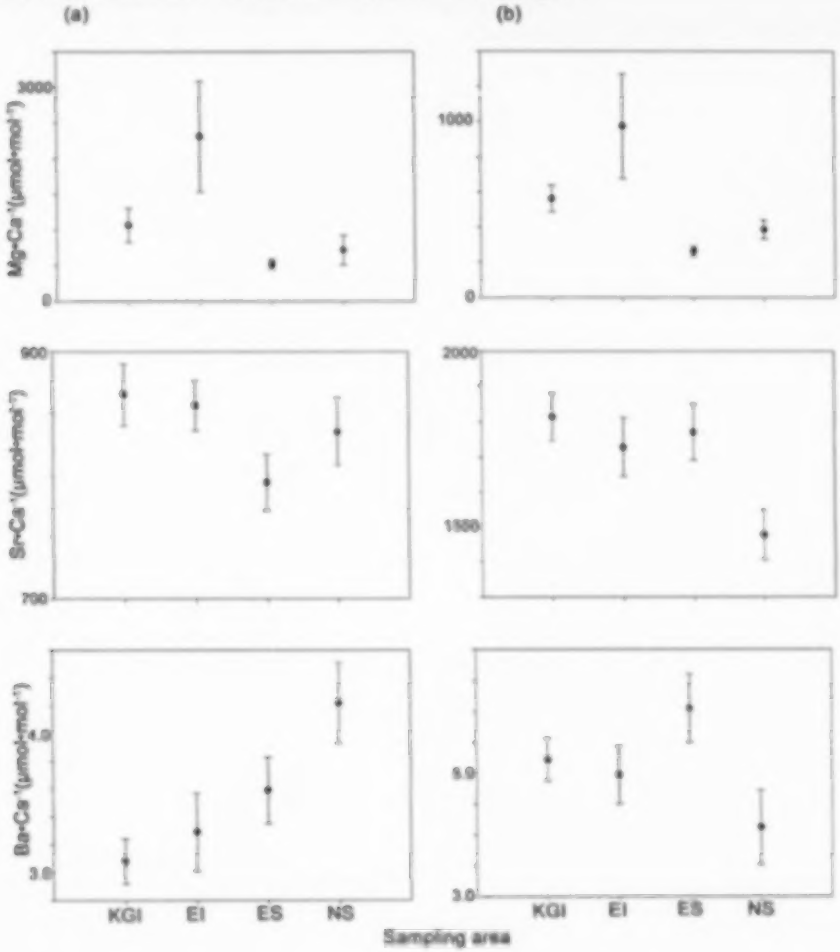
Population structure and connectivity in Scotia Sea icefish

Otolith chemistry showed strong evidence of a population boundary, discounting hypotheses of early life connectivity between Scotia Sea icefish off the northern Antarctic Peninsula and South Georgia. Similar nucleus chemistry at sampling areas off South Georgia suggested a discrete, locally recruiting population, consistent with larval assemblages (North and Murray 1992) and evidence from growth rates (Gubsch 1980; Kompowski 1990; La Mesa et al. 2004), meristics and morphometrics (Kock 1981), and parasite infestations (Siegel 1980). Even though our Lagrangian modelling did not include any diel vertical migration and assumed that the effect of any active movement contributed only to residual error, our simulations corroborated the otolith chemistry, indicating that the physical circulation alone was sufficient to explain the population boundary. Contrary to previous circulation modelling (Fach and Klinck 2006; Thorpe et al. 2007), our simulations predicted that fish displaced directly from breeding grounds on the northern Peninsula in austral spring miss South Georgia and instead follow trajectories further south.

HOPS (Fach and Klinck 2006) is a high resolution (10 km × 10 km) regional model set up for the Scotia Sea that includes a feature model to correctly simulate ACC frontal locations and speeds. Run for only 1 year, it was forced with time-averaged National Centers for Environmental Prediction (NCEP) monthly wind stress field over 13 years (1982–1994) to simulate transport at a 50 m depth in austral summer during the krill spawning season only. Surface trajectories were, on average, 38.5% slower than observed drifters (Fach and Klinck 2006); in comparison, OCCAM has more realistic current time scales but, in an earlier model run (Thorpe et al. 2005), overestimates the geostrophic velocity and baroclinic transport associated with the SACCF. Drifter trajectories differed between the two models because, in the earlier OCCAM output, the Southern ACC Front and Southern Boundary, although well within observed positions east of 40°W, were further south than observed between 60°W and 40°W (Murphy et al. 2004). As a result, the simulations, averaged over the upper 200 m of the water column, indicated a lower probability of transport to South Georgia (Thorpe et al. 2007).

Nevertheless, like with HOPS, the earlier OCCAM simulations identified regions along the western Antarctic Peninsula as sources of transport to South Georgia. This was probably due to Ekman transport northward that moved particles into faster-flowing currents offshore. The probability of reaching South Georgia increased when a shallower depth-weighted mean (64 m) was used and when surface interactions with northward ice movement were included (Thorpe et al. 2007). Compared with these OCCAM simulations, our drifters for *C. aceratus* were released from nests much deeper (130–320 m) and at the end of winter (mid-October) in a newer, improved model run of OCCAM (Renner 2009; Renner et al. 2009). The main difference from the output used in the earlier studies (Murphy et al. 2004; Thorpe et al. 2005; Thorpe et al. 2007) is that the SACCF and Southern Boundary are further north in a more realistic position due to improvements in the model formulation (Renner 2009; Renner et al. 2009). In addition, the model

Fig. 5. Mean elemental ratio concentrations found in the otoliths of *Chaenocephalus aceratus* from the Southern Ocean. Bars show standard error. Data for $Mg{\cdot}Ca^{-1}$, $Sr{\cdot}Ca^{-1}$, and $Ba{\cdot}Ca^{-1}$ are from otolith (*a*) nuclei and (*b*) edges.



was forced with 6-hourly wind stress data, and the trajectories may have reflected seasonal displacement of the wind field.

In further simulations using this new OCCAM run (not shown here), we found a number of trajectories near South Georgia with releases concentrated in the summer months. More importantly, however, the further north that a particle was released, the higher was the chance of reaching South Georgia. As a result, *C. aceratus* larvae leaving nests from King George Island follow trajectories to the western shelf of the South Orkney Islands. In contrast, larvae leaving nests at depth from Elephant Island during early spring are transported north of the South Orkney Islands but south of South Georgia as the wind field displaced particles southward. Both sets of trajectories are consistent with the heterogeneity that we found in the nucleus chemistry between the two regions.

On the other hand, finer-scale heterogeneity in the nucleus chemistry between King George Island and Elephant Island may have been the result of mixing between fish exposed to Bransfield Strait water and others recruiting from shelf areas (e.g., Kellermann 1989). Alternatively, an episodic influx of larvae transported from further south along the western Peninsula is more consistent with the complex pattern of temporal and spatial differentiation found in the microsatellite data around the northern Peninsula and South Orkney Islands (Papetti et al. 2007, 2009). However, physically generated variability associated with the CC and ASF in early life connectivity from the tip of the Antarctic Peninsula to the South Orkney Islands, Elephant Island, and King George Island would also help explain the differentiation found in the otolith chemistry and genetic data, as well as the striking fluctuations in age-class frequencies between years (Kock and Jones 2005).

Otolith chemistry on the Antarctic Peninsula and at South Georgia

Circulation models greatly enhance the construction of hypotheses like these by generating predictions that can be examined in the field. Unlike the frequency data generated

by genetics, meristics and morphometrics, or population-level growth estimates, the multivariate data from otolith chemistry are amenable to powerful tests of these predictions using analysis of variance. In *C. aceratus*, Mg-Ca^{-1} contrasts between the Antarctic Peninsula and South Georgia were very strong. Because Mg-Ca^{-1} is thought to be related to fish activity (Bath Martin and Thorrold 2005), higher edge Mg-Ca^{-1} at the Peninsula was consistent with adult reproductive activity. High Mg-Ca^{-1} at the nucleus, on the other hand, was consistent with activity in response to jets and eddies in the complex circulation at the Peninsula. In previous studies (Ashford et al. 2005, 2007), Mn-Ca^{-1} was associated with resuspension or authigenic activity on the Patagonian Shelf. However, in the Antarctic, concentrations were generally near detection levels, similar to our results for *C. aceratus*.

Sr-Ca^{-1}, linked to differences in growth as a result of water temperature and food availability (Campana 1999), previously distinguished CDW from colder water (Ashford et al. 2005, 2007). Enriched edge Sr-Ca^{-1} in *C. aceratus* east of South Georgia suggested a larger proportion of CDW mixing with shelf waters than to the north. This was supported by edge Ba-Ca^{-1}, which reflects ambient concentrations of dissolved Ba (e.g., Campana 1999). Accumulating as insoluble barite in the open ocean of the ACC (Dehairs et al. 1992), Ba is transported to depth in biogenic debris; bacterial activity releases the barite crystals between 200 and 700 m, where they accumulate and dissolve (Stroobants et al. 1991; Dehairs et al. 1997). As a result, enrichment of both edge Sr-Ca^{-1} and Ba-Ca^{-1} east of South Georgia and at Elephant Island and King George Island was consistent with the proximity of the SACCF, flooding the shelf with CDW transported from open water.

These relationships with hydrography are important for understanding how otolith chemistry can be used to address ecological questions. Generated by similar environmental conditions, a characteristic chemistry for the western shelf of the Peninsula can be used to trace connectivity to other areas downstream in the ACC but renders the technique ineffective for studying movement on the western shelf itself. However, differences in water temperature and prey availability between warmer oceanic CDW and modified CDW on the shelf, and between both these and waters in the Bransfield Strait, suggest that otolith chemistry would be useful for studying fish moving onto the shelf from the ACC or between the western shelf and the Bransfield Strait. Similarly, WDW on the South Orkney shelf suggests that the technique may be useful for examining connectivity along the southern Scotia Ridge.

Testing early life connectivity

Extended larval phases, common in notothenioids, accentuate their vulnerability to advection, potentially generating large-scale connectivity between shelf regions along the ACC. Our simulations suggest that the precise timing and position in the water column fundamentally influence the direction of connectivity. Nesting behaviour in icefish species (e.g., Kock 2005) that delays pelagic exposure until late winter – spring may result in connectivity to the southern Scotia Ridge and further east. By contrast, notothenioids that spawn at the Peninsula at similar times as *C. aceratus* may nevertheless disperse downstream to South Georgia if they release pelagic eggs that enter the upper water column during summer to be transported along the same pathways as young krill. In *Notothenia coriiceps*, a notothenioid species that releases eggs demersally that then ascend to surface waters, larval and juvenile stages have been found in oceanic waters near the SACCF between the Antarctic Peninsula and South Georgia (White et al. 1982; Kellermann 1991).

Early life history is likely to interact with the physical circulation in other ways. Observed natural meandering of ACC fronts, alternately closer and further away from the Antarctic Peninsula (Nowlin and Klinck 1986), can generate episodic transport towards South Georgia (Fach and Klinck 2006), leading to temporal variability in connectivity and potentially restricting genetic differentiation downstream (Jones et al. 2008). Long-term shifts in the wind stress field associated with climate variability (Meredith and King 2005; Gille 2008) may fundamentally alter the dynamics of populations and their abundance and persistence by modifying connectivity between shelf regions. Moreover, concentrations of 1+-year-old *C. aceratus* upstream of larval assemblages in the self-recruiting population at South Georgia imply movement from larval assemblages counter to the large-scale circulation. Active cross-shelf migration by a powerful postlarval stage may be critical in the life history of many notothenioids (Everson 1969; White et al. 1982): movement of postlarval *C. aceratus*, cued on the large-scale circulation, would also help account for gene flow from the South Orkney Islands to Elephant Island (Papetti et al. 2009).

Particle simulations help in understanding interactions like these that involve a strong physical component. On their own, however, the uncertainty involved has frequently undermined definitive conclusions. Conversely, hydrographic contrasts such as those generated along the southern Scotia Ridge by the confluence of water in the ACC and the Weddell Sea make otolith chemistry a uniquely powerful technique, but the hypotheses that it has been used to test often lack an explicit oceanographic context. Used in complement, our results show that particle simulations can provide a quantitative way of constructing hypotheses that incorporate the physical circulation, generating predictions that otolith chemistry can validate. Combining the two techniques promises an innovative approach to resolve early dispersal and connectivity related to the physical circulation of oceanic systems.

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Spatiotemporal patterns in migration timing of coho salmon (*Oncorhynchus kisutch*) smolts in North America

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Abstract: The timing of ocean entry by salmon smolts is presumed adaptive to maximize survival during this critical life transition. We analyzed the peak timing, duration, and interannual variation in timing of smolt migrations for 53 coho salmon (*Oncorhynchus kisutch*) populations from central California to Kodiak Island, Alaska. The objective was to examine potential influences of both local watershed characteristics and larger-scale processes in the marine environment on smolt migration patterns. Multivariate analyses demonstrated a strong latitudinal gradient in migration patterns with trends toward later, shorter, and more predictable migrations with increasing latitude. Cluster analysis performed on migration descriptors indicated three major population groupings that coincide with major coastal oceanic regions in the northeast Pacific: a northern group from Kodiak Island to the Queen Charlotte Islands, British Columbia, a central group from the Queen Charlotte Islands south to the Columbia River, and a southern group from the Columbia River southward. These regional patterns transcended local variability associated with watershed characteristics and trap location, suggesting that the patterns reflect adaptation to differences in timing and relative predictability of favorable conditions in the marine environments that smolts enter.

Résumé : Le calendrier de l'entrée des saumoneaux dans l'océan est présumé être une adaptation pour maximiser la survie durant cette transition importante dans la vie des saumons. Nous avons analysé le moment des migrations maximales, la durée des migrations et la variation interannuelle du calendrier de la migration des saumoneaux dans 53 populations de saumons coho (*Oncorhynchus kisutch*) réparties du centre de la Californie à l'île Kodiak, Alaska. Notre objectif était d'examiner les influences possibles à la fois des caractéristiques du bassin versant local et des processus à plus grande échelle dans le milieu marin sur les patrons de migration des saumoneaux. Des analyses multidimensionnelles indiquent un fort gradient latitudinal dans les patrons de migration, avec une tendance vers des migrations plus tardives, plus courtes et plus prévisibles aux latitudes plus élevées. Des analyses de groupement effectuées sur les descripteurs de la migration identifient trois principaux regroupements de populations qui coïncident avec les trois régions côtières principales du nord-est du Pacifique : un groupe boréal de l'île Kodiak aux îles de la Reine-Charlotte, Colombie-Britannique, un groupe central des îles de la Reine-Charlotte vers le sud jusqu'au fleuve Columbia et un groupe austral au sud du Columbia. Ces patrons régionaux transcendent la variabilité locale associée aux caractéristiques du bassin versant et à la position du piège, ce qui laisse croire que les patrons sont le reflet d'une adaptation aux différences dans la présence et la prévisibilité relative des conditions favorables des environnements marins dans lesquels les saumoneaux vont pénétrer.

[Traduit par la Rédaction]

Introduction

The migrations of diadromous fishes between freshwater and marine ecosystems presumably evolved to allow species to exploit favorable conditions for growth and reproduction (Northcote 1978; Gross et al. 1988). Because the period of most favorable conditions in a particular environment or along the migration route to that environment is often transient, natural selection should act on migration timing so that it coincides with the most suitable conditions (Hodgson and Quinn 2002). The transition of juveniles from fresh to salt water marks a particularly critical phase in the life history of anadromous salmonids. Smolt emigration is preceded by rapid physiological, morphological, and behavioral transformations that preadapt fish for life in salt water and initiate downstream movement (Folmar and Dickhoff 1980; Groot 1982; Hoar 1988). Once in the ocean, smolts must acclimate to a radically different suite of ecological circumstances, including new food resources, new predators, and a substantially different physicochemical environment. Mortality rates of juvenile salmon during the first months at sea are high; it is generally believed that much of the total ocean

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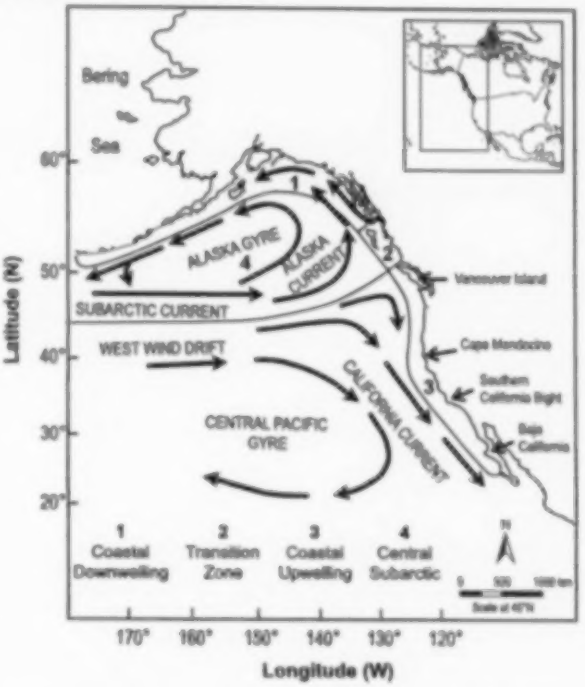
mortality incurred by salmon occurs during this period of early ocean life (reviews in Pearcy 1992; Quinn 2005; Pearcy and McKinnell 2007).

The timing of ocean entry is presumed to have evolved to maximize survival (McCormick et al. 1998). One hypothesis is that smolts are most vulnerable to predation at small sizes (Mortensen et al. 2000; Willette et al. 2001; Quinn 2005); therefore, entering the ocean when conditions (e.g., temperature, food availability) are favorable for rapid growth minimizes the time that fish are in this vulnerable size class (Holtby et al. 1990). Alternatively, it has been proposed that juvenile coho salmon (*Oncorhynchus kisutch*) that do not meet a critical size after their first summer at sea are less likely to survive the following winter because they are unable to meet minimum metabolic demands (Beamish and Mahnken 2001; Beamish et al. 2004). Timing could also be adapted to seasonal cycles in the abundance or distribution of predators (Mortensen et al. 2000), the abundance of alternative food sources for those predators (Nickelson 1986; Willette et al. 2001; LaCroix et al. 2009), or oceanic surface currents that may be important in transporting smolts offshore and away from predators (Favorite and Laevastu 1979). Whether the mechanisms controlling early marine survival result from bottom-up processes, top-down processes, or both, all of these hypotheses potentially imply the existence of a temporally limited "window of opportunity" in the ocean environment, a period when conditions for growth and survival are most favorable (Holtby et al. 1989; McCormick et al. 1998; Stewart et al. 2006). The timing and variability of such windows should exert strong selection pressure on timing of ocean entry by salmon smolts.

Across the North American range of coho salmon, the coastal environments that smolts enter are remarkably diverse, being profoundly influenced by the major oceanic surface and subsurface currents, prevailing wind directions, physiography of the coastline, and morphology of the continental shelf (Bakun 1973; Ware and McFarlane 1989). Based on differences in oceanographic and biotic characteristics, Ware and McFarlane (1989) classified the northeast Pacific into three major production domains: (1) the Coastal Downwelling Domain, which extends north and west from approximately 51°N along the southern Alaska coast and around to the Aleutian Islands and which exhibits downwelling through much of the year, (2) the Coastal Upwelling Domain, which extends roughly from 50°N to 51°N (Vancouver Island) south to Baja California and typically experiences upwelling from about March through September, and (3) the Central Subarctic Domain, which includes the offshore region bounded by the Subarctic Current on the south and the Alaska Current on the east and north and which has the Alaska Gyre as its core (Fig. 1). The boundaries of these domains vary from year to year depending on the strength of the Aleutian low pressure system in the Gulf of Alaska and the related occurrence of El Niño or La Niña events, which influence the position of the subarctic boundary and the relative amount of water advected north into the Alaska Current and south into the California Current (Mysak 1986). Consequently, the coastal region off British Columbia constitutes a Transition Zone between the Coastal Upwelling and Coastal Downwelling domains (Fig. 1). Across these coastal regions, differences in oceanography, coastal morphology (e.g., shelf width, bathymetry, and degree of isolation from off-shelf environments), and freshwater inputs suggest that the processes controlling the seasonal timing, duration, and interannual predictability of favorable conditions for coho salmon smolts are likely to vary across the species' range as well.

Fig. 1. Major surface currents and approximate boundaries of fishery production domains in the northeastern Pacific Ocean. Inset shows location off the west coast of North America. Modified from Ware and McFarlane (1989).



For the timing of smolt migrations to be synchronous with favorable periods in the ocean, two events in the freshwater environment must occur: fish must attain a state of "migration readiness" (Wedemeyer et al. 1980; Groot 1982) and they must respond to migration cues or "releasing factors" that initiate downstream movement at the appropriate time (Schreck 1982). Because smolts cannot "sample" the marine environment prior to entering it, migration patterns should reflect adaptation to long-term average environmental conditions (McCormick et al. 1998; Quinn et al. 2009). The general physiological window for smoltification is likely dictated by photoperiod, which entrains natural endogenous rhythms to produce a migration physiology in individuals that have reached the requisite state of maturity (Wedemeyer et al. 1980; Groot 1982; Hoar 1988). However, other environmental factors that vary on an annual basis can influence migration timing through effects during both the preparatory and migratory phases. These factors include water temperature, which affects developmental state and can act directly as a stimulus (Hoar 1988; Bohlin et al. 1993; Clarke and Hirano 1995), stream discharge (usually rapid increases; Bohlin et al. 1993; Spence 1995; Whalen et al. 1999), and possibly lunar phase (Grau 1982; Roper and Scarnecchia 1999; DeVries

et al. 2004). Migration cues must either serve as reliable indicators of favorable conditions in the ocean (e.g., if warmer temperatures in the stream are correlated with earlier favorable windows at sea or lunar phase is coupled with favorable tidal cycles) or signal openings in the freshwater window (e.g., suitable temperature or flow conditions) that allow for safe passage downstream. Given the heterogeneity in environmental conditions experienced by juvenile coho salmon across their North American range, as well as the potential differences in the predictability and duration of favorable conditions in the marine environment, it seems likely that the relative importance of different factors as migration cues may differ across regions as well.

In this paper, we analyze the migration characteristics of coho salmon smolts throughout much of the species' northeast Pacific range, characterizing the timing, duration, and interannual variation in timing of 53 populations from central California to Kodiak Island in Alaska. Although previous studies have noted latitudinal gradients in timing of the peak or median date of migration (Drucker 1972; Sandercock 1991; Pearcy 1992), the duration and year-to-year variation in migration timing have not been systematically examined. Our objective was to determine if broadscale regional patterns in migration characteristics exist and, if so, whether they are consistent with current understanding about windows of opportunity in nearshore coastal environments that smolts enter. Because such patterns have the potential to be obscured by variation in environmental conditions in freshwater or by factors such as the position of migrant traps within the stream network (e.g., interior headwater streams versus mainstem near-ocean locations), we sought to account for these influences as well.

Materials and methods

Smolt migration data

Downstream trapping data for coho salmon were compiled from published and unpublished sources for 53 streams from central California to Kodiak Island, Alaska (Table 1). Sites were selected based on the availability of at least 3 years of migration data so that we could evaluate interannual variation in migration timing. Most populations included in the analysis consisted only of wild fish; however, some streams were included that had received plants of hatchery fish at various points in their history. In a few instances, we included data from populations where hatchery fish were being planted during the period of sampling if the number of hatchery fish was believed to be small relative to wild population or the hatchery fish planted were from local broodstock. These exceptions were made to provide samples in geographic regions that were otherwise poorly represented in the data set. Sampling duration in individual study streams ranged from 3 to 17 years and occurred over the period from 1934 to 2007. Intensity of sampling, the type of traps used, and the efficiency of trapping all varied among data sets. A detailed list of data sources can be found in Spence (1995).

Derivation of daily estimates

For the majority of streams, available data were in the form of daily smolt counts or estimates (adjusted for trap efficiency), and these daily values were used whenever possible. For the remaining streams, data were available only as 5-day or 7-day total counts or estimates. In these instances, we derived daily estimates by dividing the total number of migrants by the number of sampling days. Trapping for a few streams in Oregon and California occurred year-round. For these streams, we counted as smolts only fish migrating after 15 January, as there were typically few migrants in January but no consistent breaks in downstream movement after that date. Furthermore, in an Oregon stream, coho salmon migrating prior to February did not show elevated gill Na^+,K^+-ATPase activity or other indicators of physiological change associated with smoltification (Rodgers et al. 1987).

For days where counts were missing, either because of the sampling regime or as a consequence of washouts during high-flow events, counts for the days immediately preceding and following the unsampled period were averaged to derive an interpolated daily estimate. If traps were fished continuously but smolts were tallied less often than once per day, the total catch was divided by the number of sampling days to obtain a daily estimate. If prolonged washouts or trap malfunction occurred (i.e., more than 3 or 4 days), data for the entire year were excluded. The decision to discard data was subjective and depended on when the data gap occurred relative to the peak of migration and the proportion of the total number of fish that likely moved downstream during the washout. For any stream and year, if the peak of migration was not clearly discernible or occurred within 1 week of the onset or termination of sampling, the data were discarded to reduce the possibility of retaining years for which the true peak occurred outside of the sampling interval.

Migration variables

For each stream, the timing of smolt migration and its variation were characterized with five statistics (Table 2). Two statistics were used to describe the central tendency of timing of migrations: the median date of migration and the date of peak migration, the latter being defined as the midpoint of the 5-day interval during which the greatest number of fish emigrated. We included both variables in the analyses for two reasons: first, populations exhibiting similar median dates of migration might have very different patterns of migration (i.e., unimodal versus multimodal), and second, sampling at many sites tended to be truncated in the early portion of the run due to the difficulty of operating traps during high-flow conditions, which could lead to bias in estimating median dates of migration. Three metrics of variation in timing were estimated. Intra-annual migration dispersion, defined as the temporal scatter of individual fish around the date of central tendency in a given year, was described by (*i*) the range, in days, of the interquartile and (*ii*) the number of 5-day intervals in which total fish numbers equaled or exceeded 20% of the estimated count during the interval of the migration peak (INT20). Again, we included the latter term to provide a measure that was less affected by truncated sampling. Between-year variation was described as the standard deviation of the estimated date of peak migration. Derivation of each of these variables required slightly different treatment of the data. Variable definitions and criteria for inclusion are provided in Table 2. For statistical analyses, mean

Table 1. Geographic coordinates and years of sampling for study streams used in analysis of geographic variation in coho salmon (*Oncorhynchus kisutch*) smolt migration characteristics (data sources listed in Spence 1995).

No.	Stream	State/Province	Latitude (°N)	Longitude (°W)	Years of sampling
1	Hidden Lake	Alaska	60.46	150.20	1978–1992
2	Berners River	Alaska	58.97	134.99	1989–1992
3	Yehring Creek	Alaska	58.50	133.78	1987–1989
4	Auke Creek	Alaska	58.38	134.64	1983–1991
5	Karluk River	Alaska	57.44	154.11	1961–1967
6	Sashin Creek	Alaska	56.38	134.65	1943–1944, 1949, 1954, 1956–1964, 1968–1969
7	Porcupine Creek	Alaska	56.13	132.65	1977–1979
8	Hugh Smith Lake	Alaska	55.10	130.71	1986–1992
9	Lachmach River	British Columbia	54.30	128.89	1987–1991
10	Tally Creek	British Columbia	52.16	127.80	1949–1950, 1952–1960
11	Hooknose Creek	British Columbia	52.12	127.84	1948–1961
12	Lower Keogh River	British Columbia	50.67	127.35	1978–1987
13	O'Conner Creek	British Columbia	50.54	127.23	1977–1978, 1986
14	Upper Keogh River	British Columbia	50.54	127.21	1977–1980
15	Black Creek	British Columbia	49.85	125.10	1978–1979, 1985–1989
16	Trent River	British Columbia	49.64	124.93	1985–1989
17	French Creek	British Columbia	49.34	124.38	1986–1989
18	Coghlan Creek	British Columbia	49.12	122.57	1978–1980, 1986–1989
19	Salmon River	British Columbia	49.12	122.57	1979–1980, 1986–1989
20	Salwein Creek	British Columbia	49.09	122.05	1976–1978, 1982
21	Street Creek	British Columbia	49.09	122.02	1976–1978
22	Ryder Creek	British Columbia	49.08	121.88	1976–1978
23	Carnation Creek	British Columbia	48.92	125.00	1971–1977
24	Little Pilchuk Creek	Washington	48.06	122.04	1975–1987
25	S. Fk. Skykomish River	Washington	47.80	121.55	1978–1982
26	Harris Creek	Washington	47.68	121.91	1979–1980, 1982–1987
27	Big Beef Creek	Washington	47.65	122.73	1975–1991
28	Lost Creek	Washington	47.59	122.73	1979–1987
29	Wildcat Creek	Washington	47.59	122.73	1979–1987
30	Bear Creek	Washington	47.50	122.81	1978–1987
31	Courtney Creek	Washington	47.47	122.83	1978–1987
32	Union River	Washington	47.47	122.82	1979–1981
33	Little Tahuya Creek	Washington	47.44	122.95	1978–1987
34	Big Mission Creek	Washington	47.43	122.87	1981–1987
35	Minter Creek	Washington	47.37	122.70	1940, 1942, 1944–1946, 1948, 1950–1951, 1953–1956
36	Mill Creek	Washington	47.19	123.10	1976–1981
37	Deschutes River	Washington	47.01	122.90	1977–1991
38	Goat Creek	Oregon	46.18	123.52	1954–1959
39	Spring Creek	Oregon	45.58	123.54	1949–1958
40	Moon Creek	Oregon	45.31	123.70	1988–1993
41	East Creek	Oregon	45.30	123.68	1988–1993
42	Fish Creek	Oregon	45.16	122.15	1987–1993
43	Flynn Creek	Oregon	44.54	123.85	1960–1973
44	Deer Creek	Oregon	44.53	123.88	1960–1973
45	Needle Branch	Oregon	44.51	123.85	1960–1966
46	East Lobster Creek	Oregon	44.25	123.64	1988–1993
47	South Lobster Creek	Oregon	44.25	123.64	1988–1993
48	Hare Creek	California	39.40	123.77	1999–2003
49	N. Fk. S. Fk. Noyo River	California	39.40	123.68	1998, 2002–2006
50	S. Fk. Noyo River	California	39.39	123.68	1998, 2000–2007
51	Caspar Creek	California	39.35	123.77	1964, 1988, 1991–1992, 1994–1999, 2002–2006
52	Little River	California	39.28	123.78	1987–1989, 1991, 1993–1994, 1996–1999, 2002–2007
53	Waddell Creek	California	37.11	122.27	1934–1942

values of the five migration variables over all years of record were calculated for each population.

Watershed data

Our general purpose was to examine latitudinal gradients in migration characteristics while accounting for other sources of variability related to watershed characteristics that might obscure more general geographic patterns. We quantified 12 physical descriptors of study streams and their contributing watersheds that might explain variability in timing, dispersion, and interannual variation of smolt migrations. These variables included several indicators of watershed

Table 2. Definitions of five variables used to characterize migration patterns of coho salmon (*Oncorhynchus kisutch*) smolt populations and criteria for inclusion in the database.

Variable	Definition	Criteria for inclusion
Peak date	Midpoint of 5-day interval of maximum migration (day of year)	Peak clearly apparent, occurs more than 7 days from first and last days of sampling
Median date	Day of year on which the 50th percentile was reached	Count during the first and last 5-day sampling intervals <10% of the count during the peak interval
Interquartile range	Number of days in interquartile (i.e., days between the 25th and 75th percentiles)	Same as for median date
INT20	Number of 5-day intervals where the count equaled or exceeded 20% of the count during the peak interval	Count during first and last 5-day sampling intervals <20% of the count during the peak interval
SD peak date	Standard deviation of peak date	Same as for peak date

Table 3. Watershed variables and their expected influence on coho salmon (*Oncorhynchus kisutch*) smolt migration characteristics.

Variable	Hypothesized effects on migration characteristics
Latitude (decimal degrees)	Latitudinal gradients in stream temperature and hydrologic regimes may influence timing, dispersion, and interannual variation in migration timing
Drainage area (km^2) Stream length (km) First-order tributaries (count) Second-order tributaries (count) Third-order tributaries (count) Fourth-order tributaries (count) Fifth-order tributaries (count)	These variables serve as indicators of watershed size. Larger watersheds encompass a wider array of environmental conditions, and smolt migrations may include a number of discrete breeding groups that differ in their migration characteristics. Consequently, larger streams or those with more contributing tributaries might be expected to have more protracted migrations. Larger watersheds are more likely to include higher elevations, possibly resulting in later migrations
Highest elevation in watershed (m) Elevation of highest point of mainstem (m) Elevation of smolt trap (m)	Elevation-related variables, especially in concert with latitude, may indicate whether hydrologic regimes are rain or snow dominated. Snow-dominated systems may tend to have more predictable temperature and hydrologic regimes, which may lead to later migrations of shorter duration. Timing might also be more predictable among years in snow-dominated systems
Distance from trap to ocean (km)	Distance of trap to the ocean may influence travel time of migrant smolts. Migrations from interior tributaries may be for dispersal rather than smolt migrations. Potential interactions with latitude

size, elevation, and distance from the ocean. The rationales for their inclusion in the analysis are listed in Table 3.

Derivation of physical descriptors

Watershed boundaries for each study stream were digitized from topographic maps and stored in an ARC/INFO geographic information system (GIS) (Environmental System Research Institute 1993). Each coverage was projected into both latitude–longitude coordinates and an equal-area projection. Alber's equal-area projections were used for streams in California, Oregon, and Washington, and Lambert's azimuthal equal-area projections were used for watersheds in British Columbia and Alaska. Estimates of latitude, watershed area, and mainstem length were all determined with the GIS.

All other physical variables were determined from topographic maps. Estimates of stream order and counts of first- through fifth-order tributaries were obtained from 1:64 000 topographic maps (United States Geological Survey) for watersheds in Alaska, Washington, Oregon, and California and from 1:50 000 topographic maps (Energy Mines and Resources Canada, Surveys and Mapping Branch) for sites in British Columbia. These scales provided the most consistent resolution over the entire geographic range; coverage of finer-resolution maps was incomplete, particularly in Alaska and British Columbia. In a small number of cases, 1:64 000 maps were unavailable or unreliable. In these instances, 1:24 000 maps were used to estimate variables related to stream order. Elevation estimates were derived from 1:24 000 maps, when available. Distance from the smolt trap to the ocean was determined with a map wheel; there is some margin of error in these estimates because the zone of saltwater intrusion is not fixed in space.

Statistical analyses

Multivariate and univariate analyses were performed to examine relationships between the five measures of timing and variation in timing of smolt migrations and the 12 physical variables that we hypothesized might influence migration characteristics (Table 3). For the canonical correlation and regression analyses, the data set was limited to 50 streams for which 3 or more years of migration data and complete information on all physical and migration variables were available. Three additional streams lacking data for one or more physical variables were included in the cluster analyses. All statistical analyses were performed with NCSS software (Hintze 2007).

Canonical correlation analysis

Canonical correlation analysis was performed between the five migration variables and the set of watershed variables. The procedure was used as an exploratory technique to determine relationships among certain physical characteristics of streams and migration characteristics and to suggest further univariate analyses among a select group of these variables.

Eleven of the 12 physical variables were transformed to normalize their distributions. Logarithmic (base 10) transformations were applied to measured variables (i.e., elevations, distances, and area) and square-root transformations were used for counts (i.e., counts of first- through fifth-order tributaries). Values of latitude were normally distributed and were not transformed. Of the migration variables, only the standard deviation of peak migration date exhibited a skewed distribution. We ran analyses with both the raw values and log-transformed values and found little difference between the outcomes. For ease of interpretation, only the results obtained with the untransformed data for standard deviation of peak date are presented.

Multiple regression analyses

Multiple regression analyses were performed to model each migration variable with a reduced set of watershed variables that were identified in the canonical correlation analysis as potentially important. The purpose was to examine latitudinal gradients in the migration variables, adjusted for attributes of the watersheds that might influence migration characteristics and obscure latitudinal trends.

The regressor variables were centered about their means such that the regression models were of the form

$$Y_i = \overline{Y} + \beta_1 X'_{i1} + \beta_2 X'_{i2} + \beta_3 X'_{i1} X'_{i2} + \ldots + \beta_p X'_{ip} + e_i$$

where $X_{i1} = X_{i1} - \overline{X}_1$, etc.

This form of the model reduces inflation of variance around parameter estimates arising from collinearity among the independent variables. Interpretation of the regression coefficients is identical to a conventional slope-intercept model, with the exception that β_0 is replaced with $\overline{Y}$, the unbiased estimator of Y at mean values of all the independent variables.

Sequential (hierarchical) multiple regression was employed to compare a reduced model with latitude as the only predictor variable with increasingly complex models containing all physical variables suggested as important by the canonical correlation analysis, as well as interactions between these terms and latitude. In general, variables that were related (e.g., indicators of watershed size) were tested (F tests) for significance as a group.

Cluster analysis

Clustering techniques were employed to identify natural groupings of populations based on the five measures of migration timing and variation in timing. Distinct groupings of populations by geographic location would suggest that factors operating at large scales exert influence on migration patterns that transcends linear trends associated with latitude and the influence of other watershed characteristics. Two clustering algorithms were used: a polythetic, divisive, nonhierarchical analysis (K-means; Hartigan and Wong 1979) that minimizes within-cluster variation, and Ward's method, which agglomerates clusters by minimizing a squared distance weighted by cluster size (Ward 1963). We employed these two procedures to assess the robustness of resulting groupings. For the K-means procedure, we chose a priori to evaluate three clusters, hypothesizing that large-scale ocean influences on migration timing might correspond to major nearshore production domains off the coast of North America: the Coastal Upwelling Domain, the Coastal Downwelling Domain, and the Transition Zone in between (Ware and McFarlane 1989).

Results

Latitudinal clines in migration variables

Positive relationships were observed between latitude and both peak and median dates of migration, with migrations tending to occur earlier in the southern part of the range and later in northern latitudes (Figs. 2*a* and 2*b*). Although the relationships were strong, there was variation in timing among populations at any given latitude, suggesting that local factors also influence migration timing (see canonical correlation and regression analyses for elaboration). Several populations on the central Oregon coast migrated noticeably earlier than populations in Washington and California, deviating from the general linear trend. This pattern likely reflects disproportionate representation of traps that were farther than average from the ocean in Oregon and greater representation of traps near the coast in both California and Washington. These potential influences are addressed in the regression analyses discussed below.

Migration dispersion, measured as both mean interquartile range and INT20, tended to decrease with increasing latitude in a linear fashion (Figs. 2*c* and 2*d*). In most northern populations, 50% of the total smolt migration occurred over a 5- to 10-day period on average (Fig. 2*c*). From central and southern British Columbia south to the Columbia River, the migration interval was wider, with 50% of the fish emigrating over a 10- to 21-day period. South of the Columbia River, the migration typically lasted 2 or more months, with 50% of the fish moving out over a 2- to 5-week period.

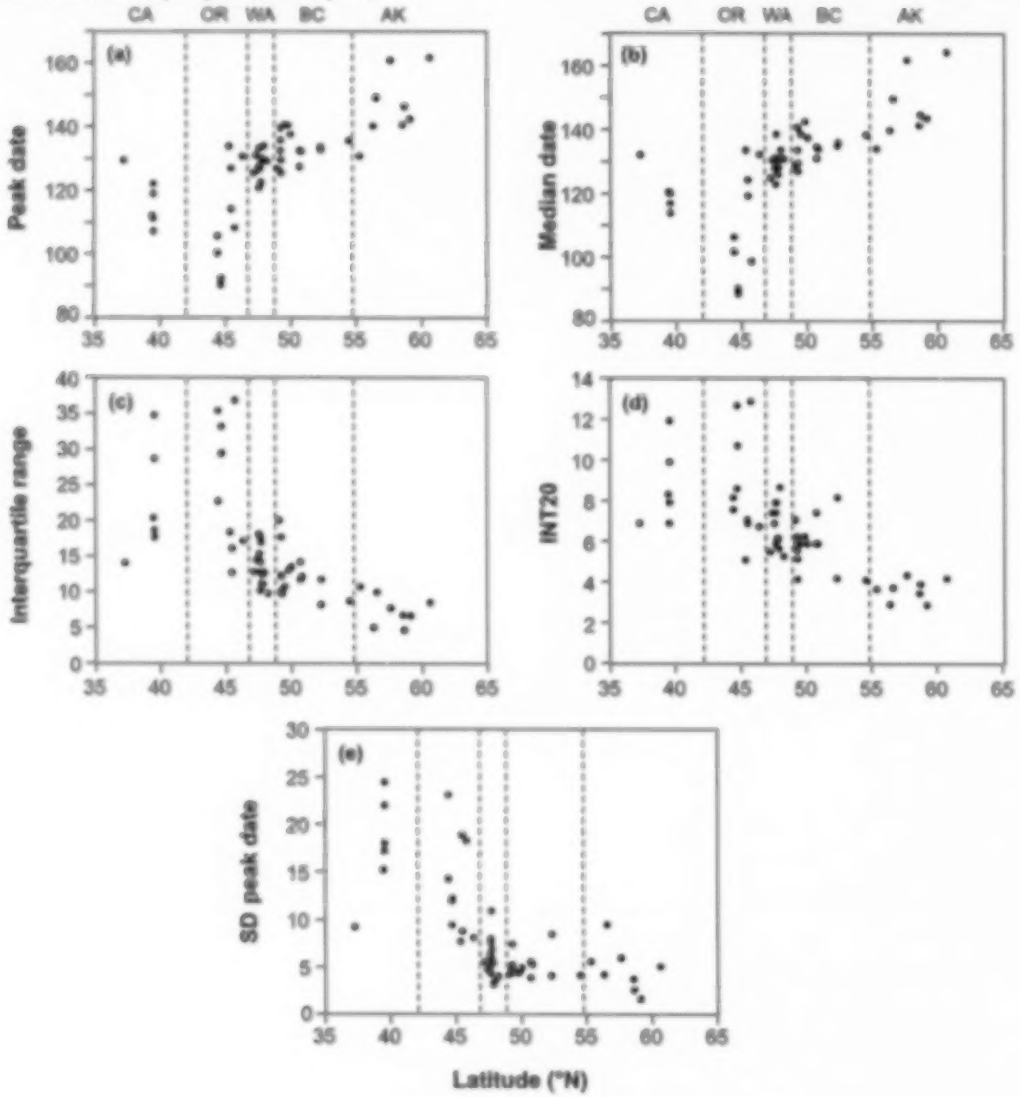
The degree of interannual variation in timing of the migration peak, measured as the standard deviation in the peak date, also decreased with increasing latitude (Fig. 2*e*). In general, for most streams north of the Columbia River, migration peaks typically occurred within the same 2- to 3-week period over all sampling years. In contrast, peak migration dates for Oregon streams often differed by 3–6 weeks among years.

Canonical correlations

Canonical correlation analysis relating the set of migration variables to the set of watershed variables indicated significant relationships between the two variable sets (F test: $p < 0.0001$). With the first canonical correlation removed, no significant relationship between the variable sets remained (F test: $p = 0.80$); therefore, the second canonical correlation was not interpreted.

The first canonical correlation was 0.92, indicating 85% overlapping variance for the first canonical variate pair (Table 4). Of the physical variables, latitude (0.85) and, to a lesser extent, $\log_{10}$ trap elevation (–0.40), $\log_{10}$ drainage area (0.39), and $\log_{10}$ stream length (0.32) correlated with

Fig. 2. Relationship between latitude and (*a*) peak date of migration, (*b*) median date of migration, (*c*) interquartile range, (*d*) INT20, and (*e*) standard deviation of peak date for 53 populations of coho salmon (*Oncorhynchus kisutch*) smolts on the west coast of North America. Peak and median dates are day of year (1 January = 1).



the first canonical variate. All five migration variables were correlated with the migration canonical variate: peak date (0.92), median date (0.89), INT20 (–0.85), interquartile range (–0.75), and standard deviation of peak date (–0.71). Thus, streams at high latitudes were associated with smolt migrations that were characterized by late timing, short duration, and low interannual variation compared with populations in the southern portion of the range. This result is consistent with the trends observed in the graphical analysis (Fig. 2). To a lesser extent, populations in longer streams, in larger watersheds, and at lower elevations also exhibited late, short, and less variable migrations, although the relationships were substantially weaker.

Multiple regressions

Hierarchical multiple regressions were used to examine relationships between each migration variable and four independent variables suggested as potentially important in the canonical correlation analysis (latitude, trap elevation, drainage area, and stream length) as well as a fifth variable (ocean distance) that appeared from preliminary analysis to interact with latitude, possibly masking its importance in

Table 4. Correlations, within-set variance (proportions of variance), and redundancies between physical and migration variables and their corresponding first canonical variates; correlations of variables with the first canonical variate of the opposite variable set are also shown.

	Correlation of original variables with their own canonical variates	Correlation of original variables with opposite canonical variates
Physical variable set*		
Latitude	0.85†	0.78†
l-Length	0.32‡	0.29
l-Drainage area	0.39‡	0.36‡
r-First-order streams	0.11	0.10
r-Second-order streams	0.07	0.07
r-Third-order streams	0.09	0.08
r-Fourth-order streams	0.14	0.13
r-Fifth-order streams	–0.03	–0.03
l-Highest elevation	0.15	0.13
l-Highest stream elevation	–0.02	–0.02
l-Elevation at trap	–0.40‡	–0.37‡
l-Distance to ocean	–0.26	–0.24
Proportion of variance	0.11	
Redundancy	0.09	
Migration variable set		
Peak date	0.92†	0.84†
Median date	0.89†	0.82†
Interquartile width	–0.75†	–0.69†
INT20	–0.85†	–0.78†
SD peak date	–0.71†	–0.65†
Proportion of variance	0.69	
Redundancy	0.58	
Canonical correlation	0.92	

*Variables preceded by "l" were $\log_{10}$ transformed. Variables preceded by "r" were square root transformed.
†>25% of the variability explained by the variable.
‡Variability explained was between 10% and 25%.

the canonical correlation. Latitude × ocean distance and latitude × trap elevation interaction terms were also considered. In each case, we fit a reduced model with latitude as the only predictor variable. We then sequentially fit models containing the set of variables associated with trap location and elevation (including interaction terms) followed by a full model with inclusion of the two additional variables related to watershed size (stream length and drainage area).

Timing

Results of the multiple regression models with peak date and median date of migration as the dependent variables were similar (Table 5). In both cases, models containing latitude as the sole predictor variable explained almost half of the observed variation in peak date ($R^2 = 0.49$) and median date ($R^2 = 0.45$). Subsequent tests indicated that trap elevation, ocean distance, and their interactions with latitude explained significant additional variation in migration timing over that accounted for by latitude alone (F test, df = 4, 44: peak date model, $p < 0.00001$; median date model, $p < 0.00001$). These models with five independent variables explained 77% of the observed variation in peak date and 79% of variation in median date (Table 5). Drainage area and stream length did not account for additional variance after the other five variables were included in the model (F test, df = 2, 42: peak date model, $p = 0.31$; median date model, $p = 0.63$).

The regression coefficients for latitude indicated that at average trap elevation and ocean distance, the peak and median dates of migration occurred approximately 2.2 days later for every degree increase in latitude. Thus, the difference in predicted outmigration timing between the northernmost and southernmost stocks in the sample is approximately 50 days. Interpretation of the coefficients for trap elevation, ocean distance, and their interactions with latitude is less straightforward, and the effects are to some degree inseparable. In general, fish from southern populations that were at higher elevations and far from the ocean tended to migrate earlier than those nearer the ocean and at lower elevations. The opposite effect was observed for northern populations, with stocks located far from the ocean and at higher elevations migrating slightly later than more coastal populations. We are cautious in this interpretation because the sample sites represented in the regression model included only some of the possible combinations of ocean distance and elevation, and the addition of new data could result in substantial changes in these parameter estimates.

Migration dispersion

Results of the two multiple regression models for describ-

Table 5. Regression of five migration variables on watershed descriptors; values indicate parameter estimates, standard errors of parameter estimates in parentheses, and p values for significance of parameters in square brackets.

Dependent variable	$\overline{Y}$	Latitude β_1	Trap elevation β_2	Latitude × trap elevation β_3	Ocean distance β_4	Latitude × ocean distance β_5	R^2	MSE
Peak date*	129.807	2.245	–0.077	0.033	0.132	–0.022	0.77	54.858
N = 50	(1.100)	(0.232)	(0.021)	(0.007)	(0.031)	(0.008)		
Model df = 5	[<0.0001]	[0.0001]	[0.0008]	[<0.0001]	[0.0001]	[0.0098]		
Median date*	131.184	2.229	–0.083	0.037	0.134	–0.022	0.79	52.356
N = 50	(1.074)	(0.227)	(0.021)	(0.006)	(0.030)	(0.008)		
Model df = 5	[<0.0001]	[<0.0001]	[0.0002]	[<0.0001]	[0.0001]	[0.0086]		
Interquartile width	15.030	–1.000	0.033	–0.014	–0.036	0.014	0.63	21.475
N = 50	(0.688)	(0.145)	(0.013)	(0.004)	(0.019)	(0.005)		
Model df = 5	[<0.0001]	[<0.0001]	[0.0161]	[0.0011]	[0.0674]	[0.0094]		
INT20	6.594	–0.259	0.013	–0.002	–0.017	0.004	0.63	1.698
N = 50	(0.194)	(0.041)	(0.004)	(0.001)	(0.005)	(0.001)		
Model df = 5	[<0.0001]	[<0.0001]	[0.0015]	[0.0913]	[0.0037]	[0.0143]		
SD peak date	8.038	–0.715	0.020	–0.008	–0.032	0.010	0.52	15.644
N = 50	(0.587)	(0.124)	(0.011)	(0.004)	(0.017)	(0.004)		
Model df = 5	[<0.0001]	[<0.0001]	[0.0914]	[0.0315]	[0.0631]	[0.0318]		

*Peak and median dates are day of year (1 January = 1).

ing interquartile range and INT20 were similar (Table 5). Models containing latitude alone explained approximately 43% (interquartile range) and 48% (INT20) of variation in migration dispersion. Subsequent tests indicated that trap elevation, ocean distance, and their interactions with latitude contributed significantly to the model after the inclusion of latitude (F test, df = 4, 44; interquartile range, p = 0.0009; INT20, p = 0.0047). The final models with five independent variables explained 63% of the observed variation in both interquartile range and INT20 (Table 5). Drainage area and stream length did not explain additional variance in either measure of migration dispersion after the other five variables were included in the model (F test, df = 2, 42: interquartile range model, p = 0.68; INT20 model, p = 0.17).

At average trap elevations and ocean distances, the models predict that width of the migration interval decreases with increasing latitude (Table 5). Interpretation of the remaining coefficients is more difficult. In general, the width of the migration interval was greater at high trap elevations and larger ocean distances but the effect was more pronounced at southern latitudes than at northern latitudes. This result is not intuitively obvious from the coefficients themselves, but the relative gain in elevation per unit distance from the ocean was generally greater in the southern part of the range (Oregon) than in more northern regions (British Columbia and Alaska); hence, the relative importance of the trap elevation and ocean distance terms tended to reverse with increasing latitude.

Interannual variation in peak date

The regression model with latitude as the only predictor variable explained 42% of variation in standard deviation of the peak date. As a group, trap elevation, ocean distance, and their interactions with latitude explained additional variation compared with the model containing only latitude (F test, df = 4, 44: p = 0.07) (Table 5). A full regression model that included drainage area and stream length did not explain significant new variation in interannual variation of peak date over a reduced model with the other five watershed variables (F test, df = 2, 42: p = 0.42).

After other watershed characteristics were accounted for, the model indicated that variation in timing of the migration peak decreased with increasing latitude. The elevation and ocean distance terms are more difficult to interpret. In general, populations farther from the ocean and at higher elevations tended to be more variable in their timing than coastal populations in the southern portion of the range. However, the reverse appeared true in the northern populations where populations far from the ocean and at higher elevations tended to be less variable, although this relationship was complicated by interactions between latitude and both ocean distance and trap elevation. We caution against overinterpreting these relationships, as not all combinations of these three variables are well represented in the data set.

Cluster analysis

The K-means cluster analysis (restricted to three clusters) based on the five migration variables produced groupings with a strong latitudinal structure. The first cluster (nine populations) consisted of seven Alaska populations as well as two northern British Columbia populations. Populations in this cluster were characterized by late smolt migrations of short duration and low variation in peak timing among years (Table 6). A second cluster (12 populations) consisted of seven Oregon populations and five of the six California populations. Populations in this cluster generally exhibited early migrations of long duration with high variability in the timing of the migration peak among years. The final

Table 6. Cluster means for three principal coho salmon (*Oncorhynchus kisutch*) population clusters derived using a polythetic, divisive, nonhierarchical clustering technique.

Stream group	Peak date	Median date	Interquartile range (days)	INT20	SD peak date
North	25 May	26 May	7.7	3.8	4.7
Middle	10 May	11 May	13.9	6.5	6.1
South	16 April	17 April	26.9	9.5	17.3

cluster (32 populations) consisted of the southernmost population in Alaska, all remaining British Columbia populations, all Washington populations, three populations in Oregon, and a single stream from California. Populations within this cluster exhibited migration characteristics that were intermediate to the other two groupings, although more similar to the northern group than to the southern group.

The results of Ward's agglomerative analysis were identical to those generated with the K-means analysis, with one exception: the southernmost population in Alaska (Hugh Smith Lake) grouped with the other Alaska and northern British Columbia populations instead of with the central cluster dominated by southern British Columbia and Puget Sound populations (Fig. 3). The high concordance between the divisive and agglomerative methods suggests highly robust groupings.

Discussion

Geographic patterns in migration characteristics

The latitudinal clines in the median and peak dates of smolt migrations that we observed have been previously reported for coho salmon (Drucker 1972; Sandercock 1991; Pearcy 1992) as well as for other Pacific salmonids (Godin 1982; Burgner 1991). These clines have been attributed in part to latitudinal gradients in various environmental factors affecting juvenile salmon in fresh water, such as water temperature, stream discharge, or period of ice breakup on lakes (Godin 1982; Burgner 1991). Others have attributed these relationships to annual cycles in primary productivity in marine environments, which generally occur progressively later with increasing latitude along the North American coast (Parsons et al. 1966; Pearcy 1992).

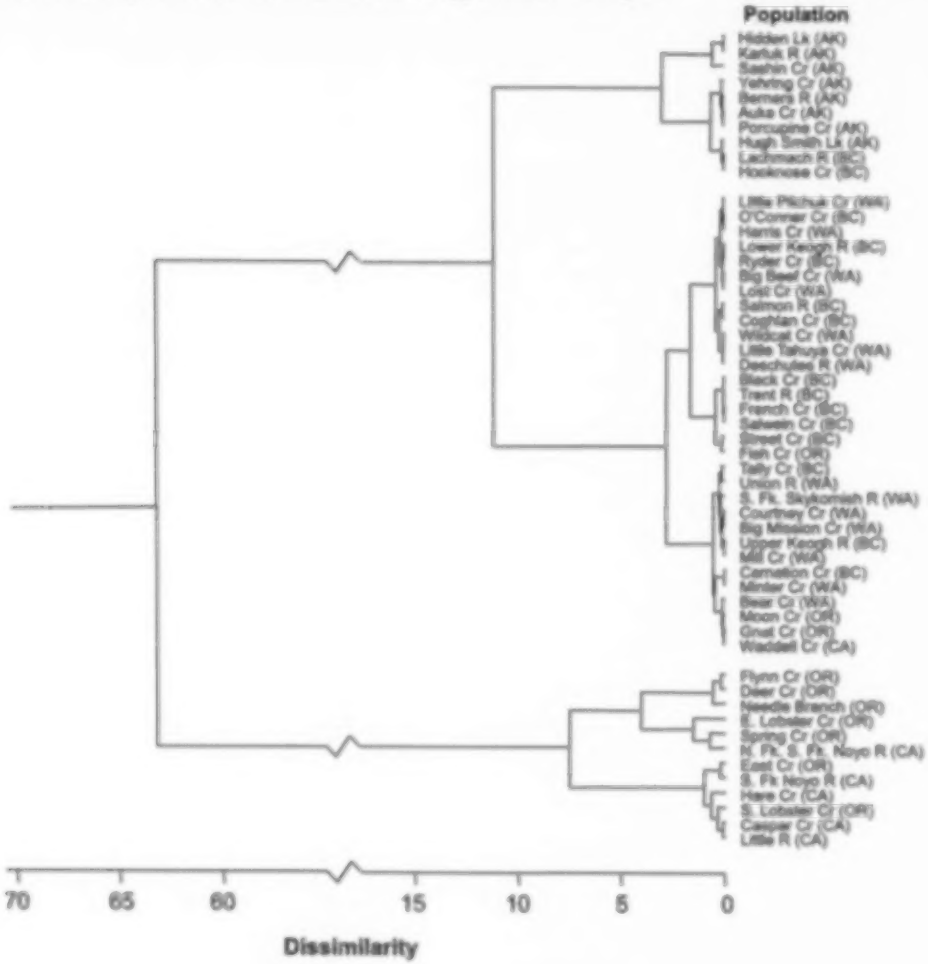
Geographic patterns in the temporal dispersion of migrations and degree of interannual variation in timing have not been systematically examined before, and our results indicate that there are gradients along these dimensions as well. Migrations of northern populations tend to be of short duration, with the majority of fish emigrating over a 5- to 10-day period surrounding the migration peak. In contrast, migrations of southern populations typically span 2–3 months, with 50% of fish moving out over a 2- to 5-week period. Populations from southern British Columbia to the Columbia River exhibit migration dispersion somewhat intermediate to these extremes, although more similar to those of the northern populations. Interannual variation in peak migration timing also increases from north to south, with a somewhat abrupt transition between Puget Sound and the Columbia River.

Although latitude explained much of the variation in each of the migration variables, we still found considerable variation in migration characteristics among populations at similar latitudes. Some of the variation in the observed timing, dispersion, and interannual variation in timing of smolt migrations was explained by the distance of the smolt trap to the ocean and the elevation at the trapping site, factors that were themselves related. At southern latitudes, populations that were relatively far from the ocean and at higher elevations tended to migrate earlier and exhibit greater dispersion and interannual variation than did more coastal populations. In northern populations, the effects of ocean distance and trap elevation on migration characteristics appeared to be small.

The specific mechanisms by which ocean distance and trap elevation influence migration variables are not entirely clear, but there are several plausible explanations. First, it is possible that differences in timing between coastal and inland populations are a simple function of the travel time from the trap site to the ocean or estuary. However, this does not explain the greater dispersion and interannual variation observed in more interior, higher-elevation sites in the south or the lack of such an effect in northern populations. Furthermore, as most of the trap locations (more than 80%) were within 60 km of the ocean, even fish passively moving downstream with the current could travel this distance in a few days. For example, coho salmon smolts in the Chehalis River, Washington, migrated at a gross rate of 28 km·day^{-1} (Moser et al. 1991). Thus, travel time alone does not appear to explain these effects. Similarly, although the correlations between trap elevation and migration characteristics could conceivably reflect the influence of elevation on environmental cues such as water temperature or flow, the range of trap elevations found in our study area was limited, with all sites falling below 300 m elevation. Thus, we do not expect that environmental gradients associated with elevation explain our results, particularly since the effects were most pronounced in the temperate zone of coastal Oregon and California where relatively small changes in elevation would have minor effects on stream temperatures or hydrology.

We believe that the most likely explanation for the significance of these variables relates to differences between northern and southern populations in the migration readiness and subsequent behavior of fish leaving upriver areas compared with fish trapped nearer the ocean. Specifically, in the southern portion of the range, where migrations from more inland populations often began in February and March and ended in May, early migrants probably spent considerable additional time rearing in fresh water before moving out to sea. Several pieces of evidence support this hypothesis. First, coho salmon migrating from Knowles Creek on the central Oregon coast in February and March did not yet exhibit physiological and morphological changes (e.g., elevated skin guanine and gill ATPase activity, reduced condition factor) that are typically associated with smoltification and that were evident in fish that migrated in April and May (Rodgers et al. 1987). Additionally, limited data from two traps on Tenmile and Cummins creeks, Oregon

Fig. 3. Dendrogram showing three principal groupings of 53 coho salmon (*Oncorhynchus kisutch*) populations based on five migration variables. Clusters derived using Ward's (1963) minimum distance agglomerative technique.

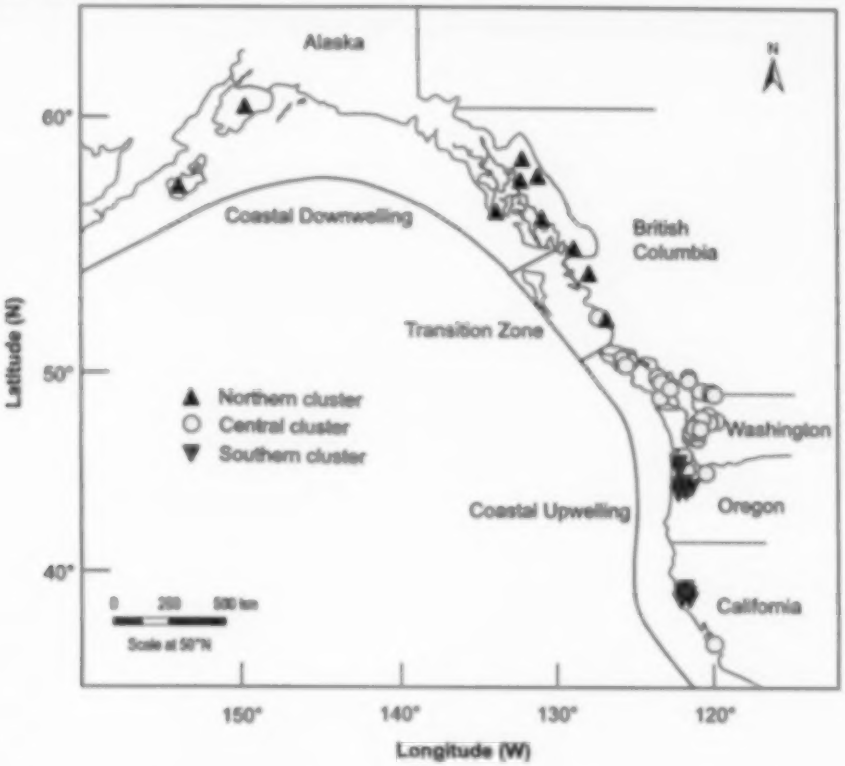


(~44°N), located less than a kilometre from the ocean indicated that, over 2 years, median migration dates were about 3 weeks later than for populations in Oregon at similar latitudes but located about 70 km inland. Similarly, median emigration dates from Carnation Creek (British Columbia) tributaries located within 2.6 km of tidewater preceded median dates at the mainstem trap at tidewater by just over 3 weeks (McMahon and Holtby 1992). All of these observations suggest that emigrants from tributaries may linger for some time in fresh water before entering the ocean.

In contrast with Oregon populations, Alaskan smolt populations that were relatively far from the coast did not move downstream earlier than near-coast populations and may have migrated slightly later. For example, populations from Karluk and Hidden lakes, 35 and 103 km from the ocean, respectively, migrated 7–10 days later than other Alaska populations where traps were located nearer to the ocean. These observations, combined with the short duration of these migrations, indicate that the behavior of inland stocks in the north differs from that of southern populations, with northern inland stocks migrating over a narrow window and apparently moving rapidly to the ocean. It is also possible that lake-rearing and stream-rearing populations exhibit different migration patterns because of different environmental cues, growth conditions, or predation risks. For example, migration timing of lake-rearing populations may be influenced by the timing of ice-out in spring, as appears to be the case with sockeye salmon (*Oncorhynchus nerka*) (Burgner 1991; Quinn 2005). Additionally, populations rearing in productive lakes may experience rapid growth in spring prior to migration, which may lead to larger size and thus higher survival at sea, attributes that may favor a delay in migration timing. The lack of interior, stream-dwelling populations among our Alaska sample sites prevents us from teasing apart these possibilities.

Despite considerable within-region variation in migration patterns attributable to watershed attributes and trap location, smolt populations exhibited distinct regional patterns in migration characteristics that transcended this local variation. This conclusion is evidenced by strong geographically

Fig. 4. Coho salmon (*Oncorhynchus kisutch*) population clusters based on migration characteristics in relation to major coastal oceanic domains along western North America.

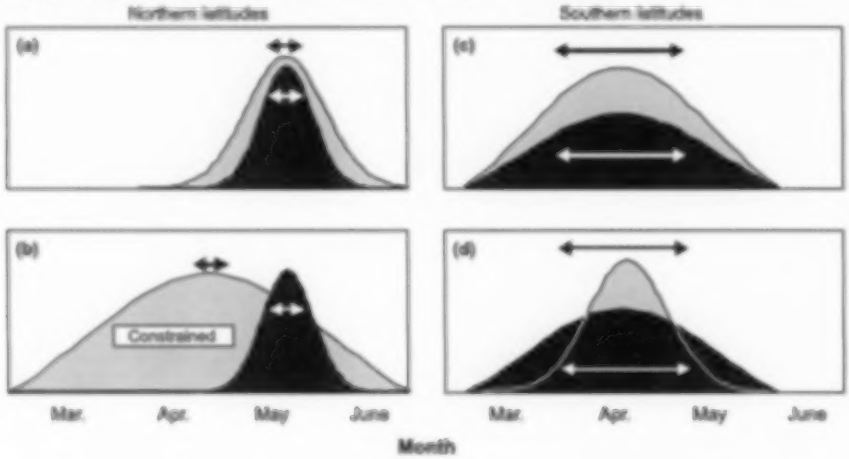


based groupings found in the cluster analyses (Fig. 4). As a group, populations entering the Coastal Downwelling Domain (north of ~54°N) migrate late in the spring over a short period of time and exhibit little interannual variation in migration timing. Most populations that enter the ocean south of the Columbia River (~46°N) migrate earlier in the spring over an extended period, with a peak migration period that is highly variable from year to year. These populations enter the ocean within the Coastal Upwelling Domain (Fig. 4). Between these two extremes, from approximately 46°N to 53°N, populations exhibit intermediate characteristics, particularly along two of three migration axes: peak timing and dispersion. These include populations entering the Transition Zone as well as populations in the northern portion of the Coastal Upwelling Domain. Significantly, almost all of the populations in our sample entering the northern Coastal Upwelling Domain do so into the relatively protected waters of Puget Sound and the Strait of Georgia and so are somewhat buffered from the immediate effects of offshore marine conditions. Thus, while the southern boundary of the central group does not align perfectly with the approximate boundary between the Transition Zone and Coastal Upwelling Domain defined by Ware and McFarlane (1989) as we originally hypothesized it might, it does coincide with a major break in the physiography of the coastline and hence the physical processes that likely control marine productivity (discussed below). These robust geographic groupings are particularly remarkable given that (*i*) outmigrant data were collected over a period spanning more than seven decades and so represent a wide range of climatic and oceanic conditions and (*ii*) trapping efforts ranged from small tributaries representing isolated breeding groups to those in larger rivers where smolt populations comprised multiple breeding groups exposed to a wide range of environmental conditions.

Migration timing and windows of opportunity

We propose that the regional differences in migration patterns observed are adaptive, reflecting differences in the timing and relative predictability of favorable conditions in the marine environments that smolts enter during the spring. Geographic variation in life history characteristics is a function of both the genetic variability of individuals constituting local populations and the spatial and temporal differences in the environmental conditions that they experience (Riddell and Leggett 1981). In this context, each of the migration variables that we quantified potentially offers different insights into how coho salmon have adapted to their environments. The mean dates of peak and median migration likely indicate long-term central tendency in the most favorable period for migration. Measures of migration dispersion may suggest the relative predictability of those favorable conditions, with narrow dispersion indicating greater environmental predictability (Holtby et al. 1989). And interannual variation in migration timing potentially reflects both genetic diversity within a population and phenotypic plasticity of individuals, which itself can be molded by selection. Cer-

Fig. 5. Schematic representation of possible relationships between windows of opportunity in the ocean (gray shading) and migration characteristics (black shading) of coho salmon (*Oncorhynchus kisutch*) smolts in (*a* and *b*) northern and (*c* and *d*) southern portions of their North American range. Black and white arrows indicate interannual variation in ocean windows and migration windows, respectively. Panels depict (*a*) a narrow, relatively invariable smolt migration in response to a window of opportunity in the ocean with similar characteristics, (*b*) a wide ocean window, but a smolt migration that is constrained during the early part of the window, (*c*) a wide and variable migration in response to a correspondingly wide and variable ocean window, and (*d*) a wide and variable smolt migration window in response to a narrow but unpredictable window in the ocean. See text for further discussion.



tainly, some of the interannual variation observed in timing and dispersion of smolt migrations represents phenotypic responses to variation in environmental variables that serve as priming and releasing factors for coho salmon while in fresh water. However, we suggest that the limits of this variability are likely dictated by windows of opportunity in the marine environment and that these windows appear distinctly different in the northern and southern portions of the coho salmon's North American range.

The late, highly synchronous, and highly predictable migrations exhibited by populations north of the Queen Charlotte Islands (54°N) might be expected to evolve under two sets of environmental conditions. First, it is possible that the characteristics of the window of opportunity in the ocean environment mirror those exhibited by migrating smolts, i.e., the window is late, narrow, and temporally predictable from year to year, and smolts migrating outside of this favorable window are less likely to survive and reproduce (Fig. 5*a*). Alternatively, the window in the ocean environment may be wider than the narrow migration dispersion indicates, but constraints within the freshwater environment could prevent smolts from exploiting the ocean early in the spring despite favorable conditions (Fig. 5*b*). Environmental constraints might include colder stream temperatures, which could slow development (and the attainment of the appropriate physiological state for migration) or inhibit migratory behavior, or physical conditions such as ice cover that may preclude or hinder downstream movement.

Consistently higher survival rates for smolts leaving during the typical peak of the migration would provide the strongest evidence of a narrow and relatively predictable ocean window of opportunity in the north. However, analyses of survival rates in relation to migration timing at temporal scales that would allow definitive testing of this hypothesis are scarce in the published literature. Lum (2003) examined survival rates of smolts leaving Auke Creek, Alaska, at roughly 1-week intervals over 5 years of record and found that, regardless of year and smolt size class, survival tended to be highest for smolts leaving during the middle 2 weeks of May, with a rapid decline in survival rate for smolts migrating after 1 June. Survival rates were significantly higher for smolts that migrated during the week of peak migration than for those that migrated during the periods before and after the peak for a single year in Porcupine Creek, Southeast Alaska (Thedinga and Koski 1984). The hypothesis of a narrow marine window of opportunity in Alaska is also supported by the fact that several populations (e.g., Sashin Creek, Karluk River, Hidden Lake, Auke Creek) with outmigrants representing multiple age classes still exhibit a relatively synchronous migration, despite the fact that smolts of different ages also differ in mean size at migration. This argues against the idea that delayed development is responsible for the later migration. Likewise, the lack of significant emigration after June, even where flows and stream temperatures appear conducive to migration, is consistent with a narrow window of opportunity in the ocean.

The fact that two populations in northern Alaska (Hidden Lake and Karluk Lake) located relatively far from the ocean migrated later than more coastal populations might suggest that constraints in the freshwater environment limit downstream movement in early spring in the north. However, this interpretation is confounded by the fact that both populations consist primarily of lake-rearing fish, which could explain the difference in migratory behavior. In both of these systems, most smolts reside in fresh water for 2 or 3 years and thus attain relatively large sizes (130–160 mm fork length) before emigrating (Drucker 1972; Dodson and Frisbie 2007). These large sizes or favorable growth opportunities in the lake environment during spring could favor a

delay in migration. In the case of Hidden Lake, ice-out typically precedes the peak of migration by several weeks, and flows are relatively stable year-round (Gary Fandrei, Cook Inlet Aquaculture Association, 40610 Kalifornsky Beach Road, Kenai, AK 99611, USA, personal communication (2008)); thus, the delayed migration does not appear to be caused by freshwater constraints.

South of the Columbia River, smolt migrations tend to occur earlier in the spring, extend over 2–3 months, and exhibit substantial interannual variation in timing. Again, there are several scenarios regarding ocean windows of opportunity that might be expected to lead to the observed migration patterns. First, the window of opportunity in the south may be longer than that in the north but vary temporally from year to year (Fig. 5*c*). Were the ocean window wide but predictable, smolts might be expected to exhibit high dispersion but low interannual variability, unless being the first through a wide window has a selective advantage or synchronous migration has evolved as a predation minimization strategy, i.e., predator saturation (Holtby et al. 1989). A second hypothesis, and the one that we believe is most tenable, is that windows of opportunity in the south are narrow and vary substantially from year to year, and that the dispersed migration pattern has evolved as a hedge against this environmental unpredictability (Fig. 5*d*). Implicit in this hypothesis is that factors in fresh water such as temperature or stream flow are generally not consistently reliable indicators of favorable conditions in the ocean; otherwise one would expect migrations to be variable in peak timing from year to year, but with narrower dispersion. As in the northern portion of the range, we had difficulty finding marine survival data collected at a fine enough temporal scale to directly evaluate the above hypotheses in the southern portion of the Coastal Upwelling Domain. However, recent evidence linking the timing of the spring transition to interannual variation in smolt-to-adult survival of coho salmon in the Oregon Production Index area (Ryding and Skalski 1999; Logerwell et al. 2003) is consistent with a highly variable window of opportunity for smolts entering the Coastal Upwelling Domain.

Within the central portion of their range, including streams entering Puget Sound and the Strait of Georgia, populations exhibited intermediate characteristics for migration timing and dispersion, but peak timing was less variable than for populations to the south. In British Columbia, hatchery smolts released 20 days apart exhibited differences in survival rate, with date of release having greater influence than size of fish at release (Bilton et al. 1984). Likewise, evidence from coded-wire tagging studies in Puget Sound streams indicates that survival of wild fish varies with time of ocean entry but that the period of maximum survival differs slightly among years (D. Seiler, Washington Department of Fish and Wildlife, 600 Capitol Way North, Olympia, WA 98501, USA, personal communication (2010)). Collectively, these observations suggest that the favorable ocean window in the central region is narrow and somewhat variable, but less so than in the southern part of the range.

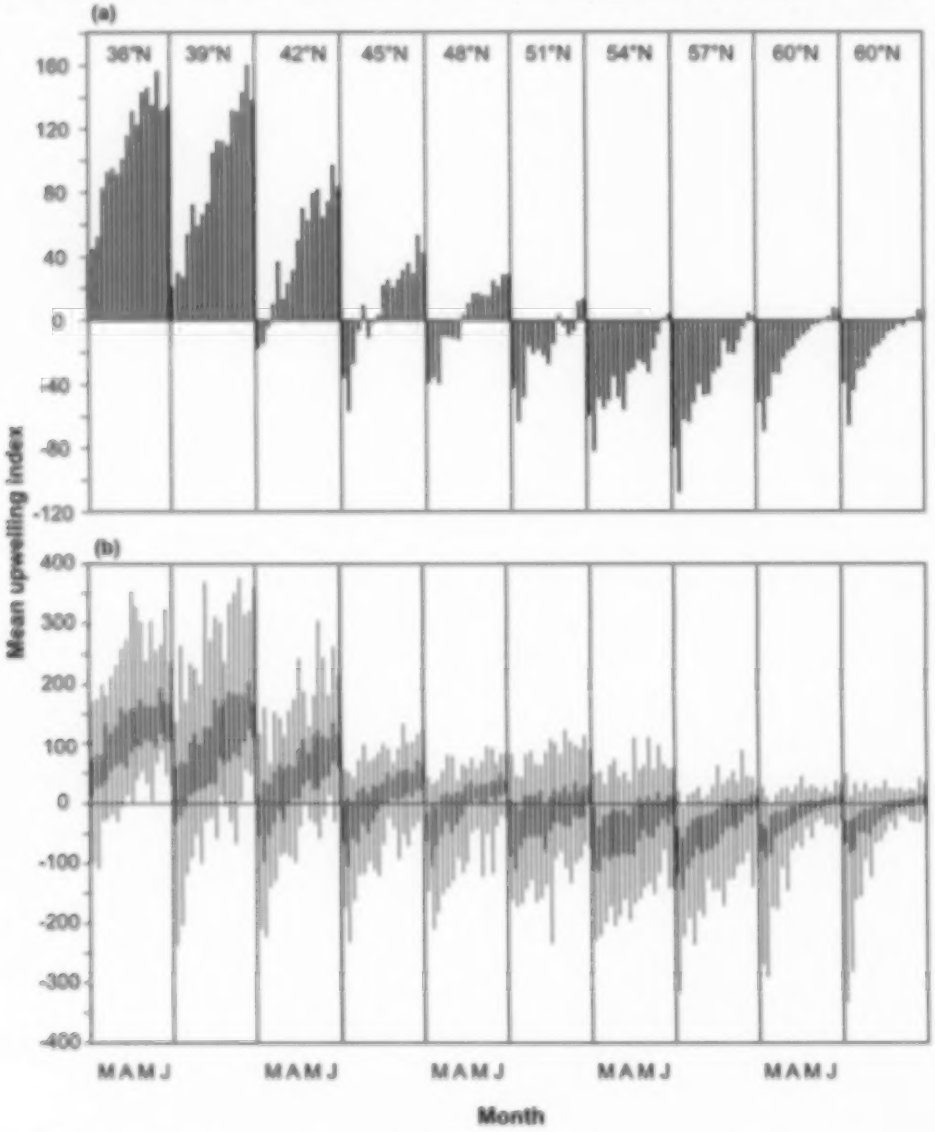
An assumption of our interpretation is that the observed phenotypic variation has a genetic basis and is not merely a function of different expression of similar genotypes due to local differences in freshwater environments. Although there is little direct evidence in the literature that the timing of downstream movements by coho salmon smolts is genetically determined, evidence exists for heritability of smolt migration timing for Atlantic salmon (*Salmo salar*) (Orciari and Leonard 1996; Stewart et al. 2006) and for time of silvering in hatchery-reared coho salmon (Saxton et al. 1984). Substantial evidence also exists for heritability in the timing of other life history events, including adult migrations (Ricker 1972; Gharrett and Smoker 1993; Hodgson and Quinn 2002) and rate of egg development, which can promote synchronous emergence of fry (Smoker 1986; Tallman 1986; Beacham and Murray 1987). Given the importance of early marine conditions on overall smolt-to-adult survival of coho salmon, there is good reason to suspect that geographic variation in smolt migration timing, at least in part, reflects underlying genetic variation.

What determines marine windows of opportunity?

If, as we assert, there are differences in the predictability of favorable marine conditions for coho salmon across their North American range, then what processes drive these differences? Very likely, differences in predictability arise from the multiple interacting factors that control ocean productivity during the springtime. These factors include (*i*) physical processes in the ocean that affect nutrient availability in the euphotic zone (e.g., currents, upwelling patterns, and tidal action), (*ii*) the physiography of the coastal region (e.g., width of the continental shelf, complexity of the coastal margin, and presence of archipelagos), (*iii*) freshwater inputs into the estuarine and coastal region (e.g., nutrient flux from rivers and effects of freshwater inflow on mixing and water column stability), and (*iv*) ambient light levels. All of these factors interact to influence primary and secondary production during the spring.

In the southern portion of the coho salmon's range, from central California to Cape Flattery in Washington, seasonal productivity in the marine environment appears closely tied to the transition from downwelling to upwelling, which occurs in late winter or early spring coincident with a shift in prevailing wind direction. Upwelling intensifies through the spring (Fig. 6*a*), bringing to the surface nutrient-rich waters that stimulate primary and secondary production, including zooplankton, neuston, and larval fishes that are important resources for newly arrived smolts (Pearcy 1992, 1997; Henson and Thomas 2007). The timing of the spring transition, however, varies from year to year, occurring as early as February or March in some years and as late as May or June in others (Fig. 6*b*) (Logerwell et al. 2003; Kosro et al. 2006; Bograd et al. 2009). Likewise, the strength of upwelling after the spring transition varies considerably among years (Fig. 6*b*) (Pearcy 1992; Bograd et al. 2009). The importance of these processes is magnified by the fact that the continental shelf is narrow (15–60 km) and the morphology of the coastline is comparatively simple (Shepard 1973). With a few notable exceptions, estuaries of coho streams along the outer coast of Washington, Oregon, and California represented in our sample are relatively small. Consequently, smolts that enter these coastal regions are more immediately and directly influenced by conditions in the open ocean. Several studies have demonstrated relationships, although complex and nonlinear, between marine survival

Fig. 6. (*a*) Estimated weekly mean upwelling indices for the period 1 March to 30 June at 10 sites off the coast of North America. (*b*) Range (thin bars) and interquartile range (thick bars) for weekly mean upwelling indices. MAMJ indicates March, April, May, and June. Latitude is indicated along the top of each graph. The two sites at 60°N are at different longitudes. Values based on a 40-year record from 1967 to 2007. Data from NOAA Pacific Fisheries Environmental Laboratory (www.pfeg.noaa.gov/products/products.html).



of coho salmon and the timing of the spring transition, the strength of upwelling during spring, or spring sea-surface temperatures, which are influenced by upwelling (e.g., Lawson 1997; Ryding and Skalski 1999; Logerwell et al. 2003).

From north of Cape Flattery (Washington) to the Queen Charlotte Islands (British Columbia), the processes driving productivity in the spring appear distinctly different from those influencing populations to the south. In this region, the continental shelf is wider (75–170 km) and the coastline is morphologically complex, owing to past glacial activity (Shepard 1973). Estuarine development is extensive and nearly all of the populations represented in our sample enter into large estuaries, straits, or fjords. Surface waters in the shelf region are generally well mixed due to the influence of major freshwater inputs, basin topography, tidal surges, and wind action (Harrison et al. 1983; Mackas and Harrison 1997; Masson and Peña 2009). From autumn to early/midspring, nutrient concentrations in the euphotic zone are typically high (i.e., nonlimiting) because of reduced stratification, sustained mixing from tidal and wind action, and relatively low phytoplankton productivity (Mackas and Harrison 1997). Consequently, the spring phytoplankton bloom in the shelf regions appears to be triggered primarily by the seasonal increase in solar radia-

tion due to increasing day length, increasing solar angle, and diminished cloud cover (Harrison et al. 1983; Gargett 1997; Li et al. 2000) rather than by episodic increases in nutrient availability, as is the case in the Upwelling Domain off California, Oregon, and the outer coast of Washington. Increases in zooplankton biomass typically lag shortly behind increases in primary production (Parsons et al. 1970; Stockner et al. 1979; Li et al. 2000), although seasonal vertical migrations of some zooplankton species such as *Neocalanus plumchrus* can occur independently of phytoplankton production (Harrison et al. 1983).

The processes influencing spring productivity in the region north of the Queen Charlotte Islands are similar to those in the Strait of Georgia and Puget Sound, but differ in some important ways. The continental shelf remains wide and the coastal margin morphologically complex, and freshwater inputs and tidal circulation continue to contribute to mixing, as in the shelf region to the south. From fall to spring, prevailing easterly and southeasterly winds drive the north-flowing surface waters of the Alaska Current coastward to produce downwelling, which typically persists throughout May and June (Fig. 6). Despite the dominance of downwelling in this region, and the relatively low contribution of nutrients from freshwater sources, the shelf region of the Gulf of Alaska is highly productive during spring. Ladd et al. (2005) proposed that the strong downwelling facilitates the flux of high-nutrient waters from offshore waters onto the shelf region. Further cross-shelf exchange is facilitated by deep basin eddies and the combined influence of strong, fluctuating tidal currents and a steep, convoluted bathymetry, factors that enhance vertical mixing (Ladd et al. 2005). As a consequence, nutrient levels in the euphotic zone remain relatively high in spring, and increases in phytoplankton production are driven primarily by increasing light levels, as occurs in the Strait of Georgia and Puget Sound (Stabeno et al. 2004). These conditions, we believe, lead to greater predictability in the timing of favorable conditions for juvenile salmon than in the Coastal Upwelling Domain to the south.

Implications

The pronounced regional differences in migration patterns of coho salmon smolts suggest that populations have evolved different strategies for dealing with the distinctly different selective regimes in the marine environments within each region. In predictable environments, populations should converge on phenotypes that consistently confer higher fitness. In unpredictable environments, no one phenotype consistently outperforms others under all environmental conditions because selection always lags behind environmental change (Garcia de Leaniz et al. 2007). In this context, smolt populations in the north appear to have adapted to a narrow but highly predictable window of favorable conditions in the marine environment by evolving a highly synchronous migration. In contrast, populations in the south exhibit a more protracted and variable migration, likely as a hedge against environmental unpredictability in the ocean. Both strategies are adaptive, but the underlying bases for adaptation will differ, predictability leading towards greater homozygosity and unpredictability leading toward greater heterozygosity or phenotypic plasticity.

Given these differences, the relative importance of different environmental cues that trigger outmigration of smolts may likewise differ among regions. For example, in the light-limited northern portion of the range, increasing day length in spring likely serves as a more reliable indicator of the onset of the spring marine production cycle than factors such as stream temperature or discharge, which exhibit greater interannual variability. This is not to imply that these other environmental factors play no role in triggering migration, as populations do exhibit interannual differences in timing. But this interannual variation is relatively small. In contrast, in the southern part of the range, where the onset of upwelling drives spring production in the ocean, photoperiod alone is likely an inadequate predictor of favorable conditions, and populations may be more responsive to other cues for emigration, such as changes in temperature and flow.

Understanding these region-specific differences in adaptive strategy is important to predicting how populations may respond to environmental change. For example, changes in global climate are predicted to produce changes in ocean circulation patterns, the timing and strength of upwelling, the depth of the mixed layer, and the timing of water mass stratification (Bakun and Weeks 2004; Pierce 2004; Rijnsdorp et al. 2009), all of which could result in shifts in the marine windows of opportunity for coho salmon smolts. In the tightly coupled systems in the north, even modest shifts in this window could have substantial negative consequences for populations that have adapted to a predictable window and thus may lack sufficient diversity or plasticity to respond rapidly to such changes. Likewise, climate change will almost certainly affect environmental factors in fresh water that influence the development of smolts (e.g., temperature, food resources) or that serve as cues for emigration (e.g., change in stream flow or temperature) (Mote et al. 2003; Stewart et al. 2004; Crozier et al. 2008). The combined effects of such changes could be to advance or delay migration timing, depending on the specific circumstances, but our results suggest that both the magnitude of the response and the underlying ability to adapt to changes may vary regionally.

Region-specific differences in migration patterns are also an important consideration in managing both populations and the habitats upon which they depend. For example, in the southern part of their geographic range, within-year variation in migration timing may provide a critical buffer that allows populations to persist given an uncertain ocean environment. Consequently, actions that constrain the expression of this diversity (e.g., habitat homogenization, temporally narrow flow-release schedules in regulated rivers, domestication selection in hatcheries) are likely to adversely affect coho salmon populations over the long term. In the northern part of the range, highly synchronous migrations suggest that local breeding groups within different parts of a watershed may have adapted in subtle ways to local environmental conditions to ensure this synchrony, as has been suggested for Atlantic salmon (Stewart et al. 2006). Alteration of temperature and flow regimes that decouple migration timing from periods of favorable conditions in the ocean could likewise adversely affect these populations.

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Designing marine reserves to reduce bycatch of mobile species: a case study using juvenile red snapper (*Lutjanus campechanus*)

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Abstract: Marine reserves have not been widely used to conserve mobile species because species abundance levels can be highly variable over space and time. Here we explore the potential for marine reserves to reduce bycatch of mobile species using red snapper (*Lutjanus campechanus*) as a case study. Bycatch in Gulf of Mexico shrimp trawls is a major source of juvenile red snapper mortality, and marine reserves may be mandated if bycatch reduction targets are not met. Using geographic information system (GIS) analyses of fishery-independent data, we investigated whether red snapper juveniles concentrate in "hot spots" and examined the trade-offs between abundance within hot spots (intensity) and predictability over time (persistence). These trade-offs allow fishery managers to tailor marine reserves to meet specific conservation goals. For red snapper, hot spots were primarily located around the 30 m isobath, with hot spots spread along the Texas coast in fall and clustered around the Texas–Louisiana border in summer. Increased intensity of hot spots led to lower persistence due to the smaller spatial area of higher intensity hot spots. Hot spots moved annually but generally persisted in the same locations over time, indicating that marine reserves could reduce red snapper bycatch. This approach provides a foundation for making informed decisions about design and placement of reserves for mobile species.

Résumé : Les réserves marines n'ont pas beaucoup servi à la conservation des espèces mobiles parce que les niveaux d'abondance des espèces peuvent varier considérablement dans le temps et l'espace. Nous examinons ici le potentiel des réserves marines dans la réduction des prises accessoires des espèces mobiles en utilisant le vivaneau campêche (*Lutjanus campechanus*) comme modèle. Les prises accessoires dans les chaluts à crevettes dans le golfe du Mexique représentent une cause importante de mortalité juvénile de vivaneaux campêches et des réserves marines seront peut-être prescrites si les cibles de réduction des prises accessoires ne sont pas atteintes. Au moyen d'analyses de données indépendantes de la pêche à l'aide du système d'information géographique (GIS), nous avons cherché à savoir si les jeunes vivaneaux campêches se concentrent en « points chauds » et examiné les compromis entre l'abondance dans les points chauds (intensité) et la prévisibilité dans le temps (persistance). Ces compromis permettent aux gestionnaires de la pêche d'ajuster les réserves marines afin d'atteindre des objectifs spécifiques de conservation. Chez le vivaneau campêche, les points chauds se situent principalement aux environs de l'isobathe de 30 m; ils se répartissent le long de la côte du Texas en automne et se concentrent autour de la frontière Texas–Louisiane en été. L'intensité accrue dans les points chauds entraîne une persistance réduite à cause de la surface spatiale restreinte des points chauds à forte intensité. Les points chauds peuvent se déplacer d'une année à l'autre, mais ils persistent généralement aux mêmes endroits dans le temps, ce qui fait que des réserves marines pourraient réduire les captures accessoires de vivaneaux campêches. Notre méthodologie fournit une base pour prendre des décisions éclairées sur la conception et la localisation de réserves pour les espèces mobiles.

[Traduit par la Rédaction]

Introduction

Marine reserves are closures of areas to fishing, diving, or other activities that impact marine resources. Marine reserves are beneficial in preserving biodiversity, protecting habitat, reducing overfishing, and increasing fisheries yield (Hilborn et al. 2004). Overall, marine reserves represent a spatially explicit mechanism for managing human involvement with a resource to produce a desired effect (Stewart and Possingham 2005). When the purpose of a marine reserve is to reduce bycatch, restrictions are placed on certain types of fishing gear or fishing is prohibited altogether. One contention regarding fishing restrictions in marine reserves is whether the benefits associated with fishing restrictions are great enough to counterbalance losses associated with foregone harvest. Therefore, the goal of marine reserves for

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bycatch reduction is to maximize the number of bycatch fish conserved while minimizing the area that must be closed to reduce losses of the target species. The efficacy of any marine reserve in meeting this objective depends on the design of the reserve and the characteristics of the protected species. Proper placement and design of reserves is critical for success (Crowder et al. 2000).

Mobility of organisms plays a large role in the design and placement of reserves. Scientists have investigated many aspects of mobility in relation to reserve design and placement, including home range (Palumbi 2004), larval dispersal (Allison et al. 1998), adult dispersal (Acosta 2002), and source–sink dynamics (Crowder et al. 2000). One emergent principle is that larger reserves are required for species with larger home ranges or more mobile larvae, while smaller reserves may be adequate for sedentary species and larvae (Botsford et al. 2003, 2009). Placement of marine reserves for mobile species is more difficult than for sedentary species, which has generally limited their use as a conservation strategy.

Advances in geographic information systems (GIS) have made it possible to investigate the use of marine reserves for mobile species. The key to a successful marine reserve for mobile species is maximizing the likelihood that a desired proportion of the population will be encompassed within a particular area at any given time. This can be accomplished by finding "hot spots" or areas where organisms concentrate above a desired threshold level. The next step is to investigate the predictability of hot spots over time. Thus, hot spots have two characteristics that must be optimized to find the best reserve: the intensity level and its persistence through time, characteristics that are linked by the spatial extent of the hot spot. Intensity defines the level of concentration of organisms in the area. Persistence is the number of years out of the time series that hot spots occur in the same location. We hypothesize that more-intense hot spots will be smaller in area than less-intense hot spots for mobile species that do not depend on sedentary habitat features. The smaller area of more-intense hot spots will translate into a lower probability that hot spots will overlap (i.e., lower persistence). Fishery managers can therefore select from a range of intensity and persistence levels to determine the optimal area and placement for marine reserves.

We illustrate the practical application of these concepts with a case study using marine reserves to reduce bycatch of juvenile red snapper (*Lutjanus campechanus*) in the Gulf of Mexico (GOM). The red snapper population has been overfished since the mid-1980s, and bycatch of juveniles in shrimp trawls is the major source of mortality (Goodyear and Phares 1990). The use of marine reserves is under scrutiny as a strategy for reducing bycatch. However, because bycatch of juveniles is variable in time and space because of their mobility, the level of bycatch reduction that reserves would achieve is uncertain. Our goals are to illustrate how marine reserves can be optimized for mobile species such as red snapper and to explore the decisions that managers must make when selecting an area with optimal intensity and persistence of hot spots in establishing reserves. This study therefore provides a tool for fisheries managers who need alternatives to traditional management measures. These techniques are applicable to any mobile species with a long time series of spatially referenced abundance data.

Materials and methods

Data sources

The data we used were from fishery-independent trawl surveys (Southeast Area Monitoring and Assessment Program [SEAMAP] data, www.ncddc.noaa.gov/interactivemaps/southeast-area-monitoring-and-assessment-program-sea map). The survey is conducted every summer (June and July) and fall (October and November) in the GOM and has used consistent methodology since 1987 (summer) and 1988 (fall). SEAMAP data are collected as a collaborative effort between the National Marine Fisheries Service (NMFS) and various GOM state agencies and academic institutions. The survey uses semiballoon bottom trawls with nets similar to those used in the commercial shrimp fisheries (13 m headrope, 4.5 cm mesh). Tows are conducted across depth gradients, starting and ending at a predetermined depth, so the tows are variable in duration depending on bottom topography. Almost all tows are 1 h or less in duration, but if longer, the net is emptied after 50 min (Nichols 2000). The survey region extends from 25°50′N to 30°15′N latitude and from 97°30′W to 87°30′W longitude (the Florida–Alabama border to the Mexican border) and consists of about 124 222 km^2 of survey region within the GOM. For each SEAMAP survey, 200–300 sampling stations are randomly selected each year among depth strata within the survey area; sampling within strata is weighted based on area (Nichols 2000). We used 1987–2007 data for summer and 1988–2007 data for fall in this analysis.

Only red snapper data were included in the GIS analyses. Because tow times were variable, we first calculated the abundance as the catch-per-unit-effort (CPUE). We chose the distance towed (the distance between starting and ending tow locations) to represent the unit of effort. If tow locations were not available, we estimated the distance towed by using the tow duration × the tow speed, estimated to be 3 knots (5.6 km·h^{-1}) unless stated specifically. We tested for differences in red snapper abundance by year, season, time of day, and spatial location using univariate analysis of variance (S-Plus, version 8.0.4, Insightful Corporation, Seattle, Washington). To do this, we combined CPUE data from all sampling stations. Because red snapper catches at night were significantly higher ($p < 0.05$) than during the day, daytime catches were corrected using a factor of 1.5276.

GIS methods

Because SEAMAP stations are randomly chosen each year, we first created spatially continuous surfaces from the midpoint of the sampled trawl locations, a process called spatial interpolation. Spatial interpolation estimates the value of a variable across a study area from observations taken at known locations. Many methods of spatial interpolation exist; we chose which method to use based on tests conducted on a subset of the data (S. Diamond and Y. Wang, unpublished data). For red snapper, we used ordinary kriging with a spherical model. This model is prefera-

ble to others because its structure (almost linear growth at the origin, rising to an asymptote) corresponds with spatial variation that is often observed in nature (Lloyd 2007). Kriging is a statistical method that interpolates between known values by reducing the variance of the entire data set (Myers 1997). We used Geostatistical Analyst in ArcMap (version 9.2, ESRI, Redlands, California) for all interpolations. A unique semivariogram (function of the change in variance with distance) for each seasonal and yearly data set was estimated using a cell size of 1.2 km × 1.2 km and the automatically calculated optimum values for the lag (bin) size, number of lags, partial sill (asymptote), and nugget (semivariance at a distance of zero). The cell size was set to optimize the clarity of detail. The number of neighboring stations whose data were included in the interpolation was set to 12, with at least six neighbors included. We did not include corrections for spatial trends in the data. On the resulting maps, each cell was associated with an estimated abundance of red snapper at that location.

Mapping annual hot spots

In this study, we found annual red snapper hot spots by looking for geographical areas where the interpolated abundance in a group of cells was higher than a certain threshold intensity level for each season and year of red snapper data. For each season and year, we defined four different intensity levels: (*i*) very high intensity, or red snapper abundance greater than two standard deviations (SD) above the mean, (*ii*) high intensity, or abundance greater than one SD above the mean, (*iii*) 50*A* intensity, or the area of highest abundance that summed to 50% of the total red snapper abundance in that year, and (*iv*) 75*A* intensity, or the area of highest abundance that summed to 75% of the total red snapper abundance in that year. We then created four annual hot-spot maps for each season and year, one for each intensity level. The high and very high intensity hot spots were found by including all cells with more snapper than the desired abundance threshold. The 50*A* and 75*A* hot spots were identified by an iterative procedure that summed the red snapper abundance contained in the highest abundance cells until the desired intensity threshold was reached. Using these maps, we calculated the percentage of the total snapper abundance (%RS) and the percentage of total survey area (%Area) encompassed by each annual hot spot at the four levels of intensity by season. We used the percentage of total red snapper abundance rather than the absolute number so that we could compare the differences from year to year despite differences in red snapper recruitment. We also looked at the efficiency of the annual hot spots by calculating the ratio of %RS to %Area.

Quantifying persistence

We overlaid the annual hot-spot maps by season and intensity level for the early years (1988–2000 for fall and 1987–2000 for summer) to find areas where annual hot spots persisted in the same location over time. To do this, we reclassified the cells in each annual map within a specific season and intensity level into hot-spot areas and non-hot-spot areas. Cells within annual hot-spot areas were given a code of "1" and cells in non-hot-spot areas were given a code of "0". Using Spatial Analyst in ArcMap (version 9.2, ESRI, Redlands, California), we summed the layers to create composite maps in which each cell was classified according to the number of years of persistence out of the total in the times series. The maximum number of years of persistence was 13 years for fall and 14 years for summer. We therefore generated separate composite maps, stratified by persistence, for each season and intensity level. For each combination of season, intensity level, and persistence from the composite maps, we found one or more contiguous areas of red snapper abundance that we called "composite" hot spots. Composite hot spots differed from annual hot spots in that they were based on both intensity level and persistence, rather than intensity level alone.

Marine reserve templates

We traced the outline of the composite hot spots for each combination of intensity and persistence from the composite maps to create templates for potential marine reserves. A template for a potential marine reserve was therefore the collective outline of all the composite hot spots for any given level of intensity and persistence. We evaluated the potential reserve templates, which were created from the early years of data, using the data from the later years (2001–2007). First, we quantified the ability of each marine reserve template to reduce bycatch by calculating the %RS that would have been encompassed by the templates in each later year. We calculated the total area (%Area) included in each template from the composite maps. We also measured the efficiency of each template (%RS:%Area) at each combination of intensity and persistence to evaluate the level of conservation that would have been achieved if that reserve had been closed to commercial shrimping.

Conservation goals

As an illustration of how these methods can be used as a decision-making tool for fishery managers, we arbitrarily selected two different conservation goals as examples: one based on setting a target level for fish conservation, and the other based on selecting a particular size of reserve for closure. Although specific goals have been set for reducing red snapper bycatch (Federal Register 2008), using marine reserves is part of a broader strategy that includes effort reductions, so we did not limit the conservation goals illustrated here to the mandated goals set for red snapper. The first arbitrary goal was for a marine reserve to encompass a minimum of 25% of the total red snapper abundance averaged over the entire time series. The second goal was for the conservation of red snapper based on closing a maximum of 15% of the study area to fishing. We then identified the levels of intensity and persistence that would allow us to meet each of these goals.

Results

Analysis of data

Over the time series, the number of stations averaged 270 per year for the fall survey and 247 per year for the summer survey (Table 1). The average CPUE of red snapper in fall over all years was 4.50 red snapper per kilometre towed, which was significantly higher ($p < 0.001$) than the average of 1.13 red snapper per kilometre towed found in summer.

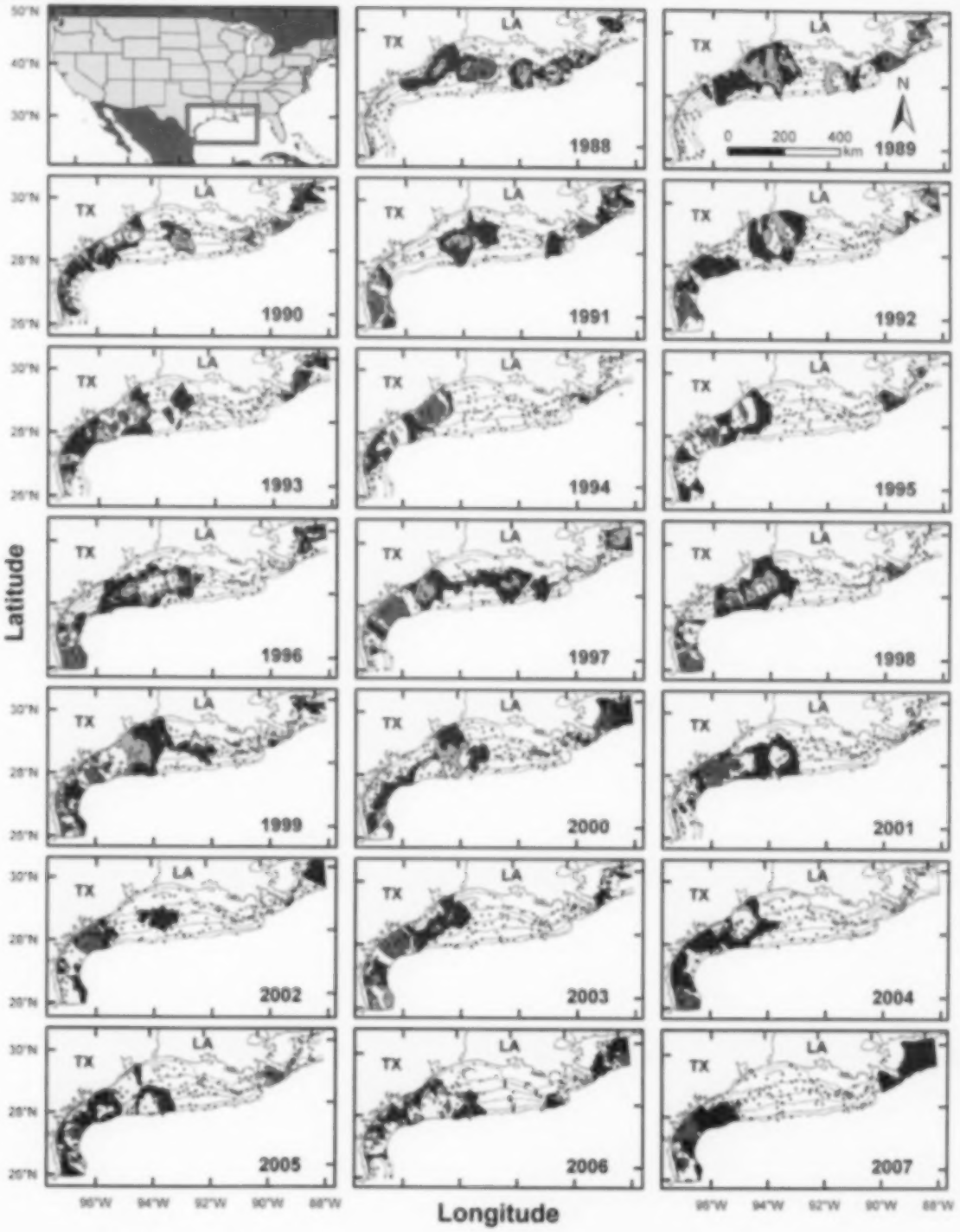
Table 1. Summary of SEAMAP survey stations and juvenile red snapper abundances in fall and summer. Fall surveys catch primarily age-0 red snapper, and summer surveys catch primarily age-1 red snapper.

			CPUE			
Year	No. of stations	% zeros	Mean	SD	CV	Maximum
Fall						
1988	277	53.4	1.87	6.93	3.70	96.06
1989	282	45.7	5.22	14.40	2.76	162.82
1990	300	40.3	4.58	13.43	2.93	142.83
1991	277	37.9	4.58	11.91	2.6	148.09
1992	256	55.5	1.12	3.29	2.94	37.64
1993	287	50.2	2.93	9.22	3.14	120.71
1994	284	40.5	5.72	13.68	2.39	103.48
1995	246	32.9	5.30	10.70	2.02	91.22
1996	323	46.4	2.44	5.02	2.06	43.37
1997	252	42.1	4.92	9.69	1.97	56.95
1998	275	46.2	2.86	6.53	2.28	61.39
1999	304	45.1	3.32	5.91	1.78	42.00
2000	291	38.8	2.85	5.47	1.92	59.07
2001	293	51.2	2.54	6.77	2.67	59.43
2002	260	46.2	3.01	7.63	2.53	90.53
2003	280	38.2	5.04	10.00	1.98	87.45
2004	225	32.0	9.22	23.87	2.59	209.98
2005	226	28.3	8.25	17.87	2.17	162.70
2006	256	27.3	6.98	12.48	1.79	89.34
2007	197	46.7	7.21	21.87	3.03	250.00
Average	269.6	42.3	4.50	10.83	2.46	105.75
Summer						
1987	276	75.0	0.76	3.06	4.03	40.51
1988	233	78.1	0.46	2.43	5.26	34.57
1989	227	80.6	1.02	7.41	7.27	105.21
1990	291	59.1	2.17	6.33	2.92	61.4
1991	279	69.2	0.97	3.11	3.22	35.49
1992	283	72.8	0.90	4.43	4.92	62.92
1993	278	71.9	0.79	2.46	3.10	19.41
1994	247	65.7	0.96	2.68	2.79	30.67
1995	245	66.1	0.82	2.09	2.55	12.58
1996	254	64.2	1.61	6.76	4.20	72.02
1997	244	62.3	1.15	4.23	3.67	55.93
1998	236	73.7	0.56	1.42	2.54	9.46
1999	257	73.5	0.65	2.97	4.57	39.25
2000	254	59.8	0.92	2.00	2.17	12.24
2001	179	76.5	1.11	6.86	6.18	89.27
2002	261	69.3	0.83	2.38	2.87	19.31
2003	207	70.5	0.65	1.99	3.07	16.47
2004	251	62.5	2.16	11.85	5.49	165.87
2005	206	59.7	2.02	6.10	3.02	46.91
2006	250	62.9	1.47	3.46	2.35	25.71
2007	232	57.2	1.80	5.02	2.79	48.30
Average	247.1	68.1	1.13	4.24	3.76	47.79

Note: % zeros, percentage of trawl stations where no red snapper were caught; CPUE, catch-per-unit-effort; SD, standard deviation; CV, coefficient of variation; Maximum, maximum CPUE at a single station.

Many of the stations had no red snapper at all, with the percentage of zero stations averaging 42.3% in fall and 68.1% in summer. Based on size, the majority of red snapper caught in fall were age 0, and the majority caught in summer were age 1. There was no correlation between the catch of red snapper in fall and summer of the same year (same conditions) or between the catch of red snapper in fall and summer of the following year (same cohort).

Fig. 1. Annual hot spots for the very high (red), high (yellow), 50*A* (green), and 75*A* (blue) intensity levels for juvenile red snapper caught in SEAMAP fall surveys. Fall surveys catch primarily age-0 red snapper. The hot spots with higher intensity are shown on top of the hot spots with lower intensity because of their smaller spatial area. Depth contours shown are 10, 20, 30, 50, 75, and 100 m. Dots show the locations of trawl survey stations.



Evaluation of annual hot spots

In both seasons, the locations of the annual hot spots from the four intensity levels often overlapped (Fig. 1). The very high intensity hot spots were the smallest of the four, whereas the 75*A* hot spots were the largest. There was no significant difference between the spatial extent of fall and summer hot spots within the same intensity level ($p > 0.05$). The high intensity and 50*A* hot spots were closest to each other and intermediate between the other hot spots in both size and location. In fall, the locations of annual hot spots for the four intensity levels showed two distinct patterns: either hot spots were scattered across the northern GOM or they were concentrated off Texas. Very high intensity hot spots were usually located off the central or lower Texas coast, with smaller hot spots immediately east or west of the Mississippi delta (Fig. 1). In summer, hot spots from all intensity levels were most often located near the Texas–Louisiana border (Fig. 2).

The %RS contained in the annual high and very high intensity hot spots was lower in the fall than in the summer (Fig. 3). In fall, the %RS in the very high intensity annual hot spots averaged 19.9%. The %RS in the fall high intensity annual hot spots followed a similar temporal pattern to the very high intensity hot spots, but averaged 40.7% over the time series. In summer, the %RS in the very high intensity annual hot spots averaged 24.7%, whereas the %RS in the high intensity annual hot spots averaged 46.9%. The 50*A* and 75*A* hot spots for fall and summer contained an average of 50% and 75% of the red snapper in the total area as expected, but this amount varied slightly each year due to the discrete nature of the bin size in the interpolation process (Fig. 3).

During both seasons, the area of the 75*A* annual hot spots varied more than the areas of the hot spots of the other intensities. There did not appear to be much of a directed temporal trend in the spatial extent of the hot spots in either season, although all four intensity levels in both seasons showed a somewhat cyclical pattern of smaller annual hot spots about every 1–3 years (Fig. 3). In the fall surveys, the average spatial area of the annual hot spots ranged from 5.1% of the survey area in the very high intensity hot spots to 41.0% of the study area in the 75*A* hot spots. The average aerial extent of the annual hot spots in summer ranged from 5.1% of the survey area in the very high intensity hot spots to 32.5% of the total survey area in the 75*A* hot spot.

The efficiency (%RS:%Area) of the annual hot spots was lower and less variable in fall than in summer, regardless of intensity level (Fig. 3). The trends in fall and summer efficiencies were almost opposite to each other during the 1980s and 1990s, although this pattern did not continue into the 2000s. Years of low efficiency in summer showed high efficiencies in fall, although a cyclical pattern with a period of 2–4 years was seen in both seasons. The highest efficiencies were shown by the very high intensity level in both fall and summer, with similar efficiencies in the high intensity and 50*A* hot spots and lowest efficiency in the 75*A* hot spot regardless of season.

Evaluating persistence

For both seasons, the composite maps of the high and the 75*A* intensity levels showed a higher number of years of persistence than the composite maps for the very high and the 50*A* intensity levels, respectively. The 75*A* composite maps showed the highest possible levels of persistence (13 years of persistence in fall and 14 years of persistence in summer), indicating that the annual 75*A* hot spots overlapped every year in fall and summer. However, the composite hot-spot area with maximum persistence was less than 1% of the total survey area in each season.

There was usually one large or primary composite hot spot for each combination of season, intensity level, and persistence, but there were often smaller composite hot spots, particularly at lower levels of persistence. The primary composite hot spots for both fall and summer were located in the northwestern GOM (for examples, see Figs. 4 and 5). In the fall, the primary composite hot spots at different levels of persistence and intensity usually started east of the Texas–Louisiana border and extended west toward the Mexican border, covering from about the 20 m isobath to the 50 m isobath (Figs. 4*a* and 5*a*). The primary composite hot spots in summer were usually centered off the upper Texas coast. They were more constrained longitudinally than in fall but usually covered more area from inshore to offshore, extending from about the 10 m depth contour to about the 60 m depth contour (Figs. 4*b* and 5*b*). Smaller composite hot spots were located immediately west of the Mississippi River delta in fall and near the Mississippi–Alabama border in both fall and summer.

Evaluating marine reserve templates

The %RS encompassed in the marine reserve templates depended on the level of intensity and persistence but in general was larger in fall than in summer at the same level of persistence (Figs. 6*a* and 6*d*). In both seasons, the percentage of the population enclosed by the templates decreased as persistence increased at all intensity levels. For both seasons and at all levels of persistence, the 75*A* template encompassed the highest percentage of the red snapper population. In fall, the 50*A* template had a higher %RS than the high intensity template, but these were very similar in summer. The very high intensity template encompassed the least red snapper (Figs. 6*a* and 6*d*).

The area encompassed by the marine reserve templates by years of persistence were similar to the patterns seen with the %RS. The area in the templates decreased as the years of persistence increased, regardless of season or intensity level. In both seasons, the percentage of the total area was greatest for the 75*A* template and lowest in the very high intensity template, regardless of the years of persistence. The areas contained in the high intensity and 50*A* templates were very similar in summer, but in fall, the 50*A* template encompassed more area, similar to the %RS (Figs. 6*b* and 6*e*).

With the exception of the very high intensity template in fall, the efficiency of the marine reserve templates increased as the percentage of years of persistence increased, generally reaching their maximum at or near the highest levels of persistence (Figs. 6*c* and 6*f*). Efficiency ratings were highest in the very high intensity templates and lowest in the 75*A* templates, with an average efficiency in fall of 1.7 and in summer of 1.9 over all levels of intensity and persistence.

Fig. 2. Annual hot spots for the very high (red), high (yellow), 50A (green), and 75A (blue) intensity levels for juvenile red snapper caught in summer SEAMAP surveys. Summer surveys catch primarily age-1 red snapper. The hot spots with higher intensity are shown on top of the hot spots with lower intensity because of their smaller spatial area. Depth contours shown are 10, 20, 30, 50, 75, and 100 m. Dots show the locations of trawl survey stations.

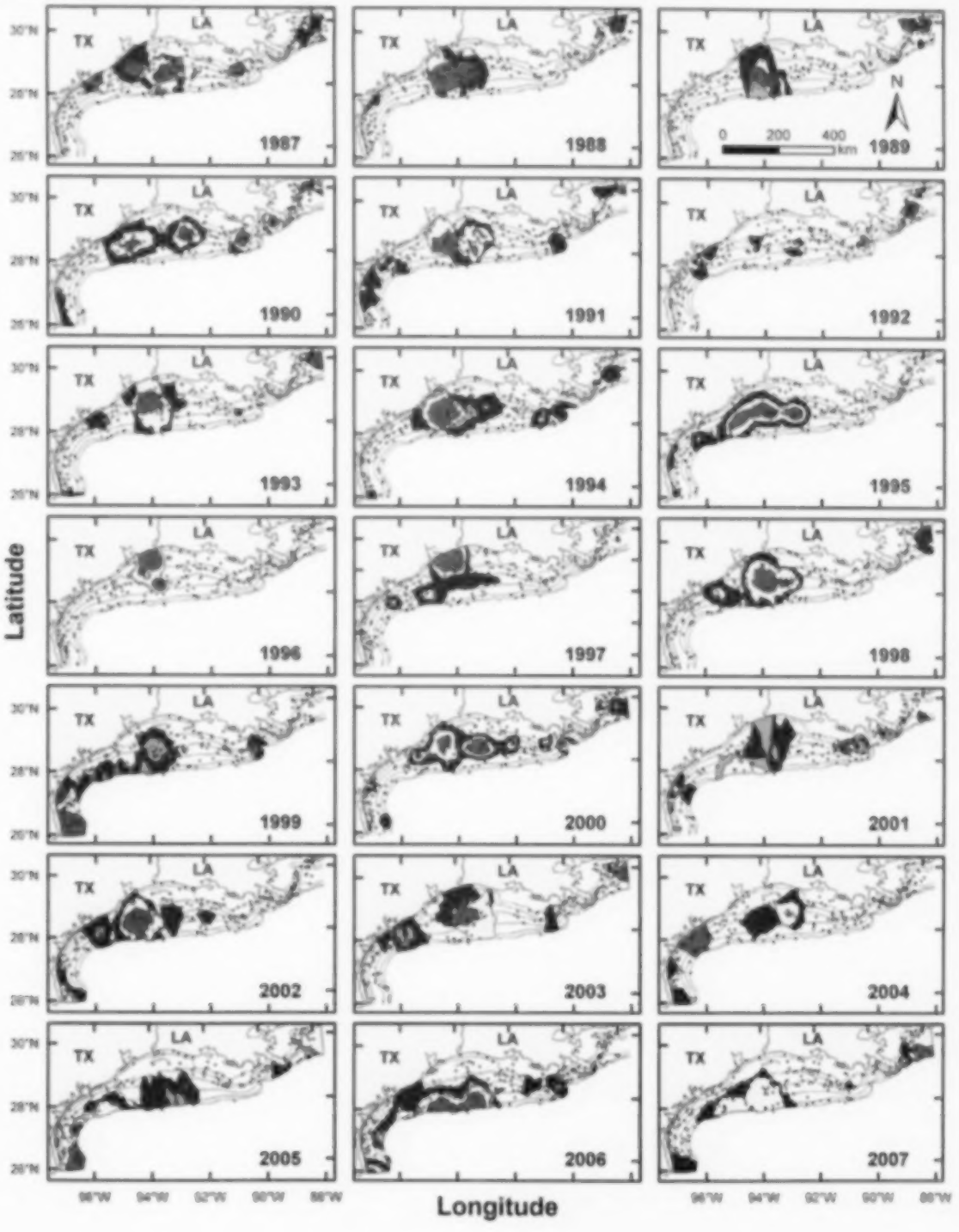
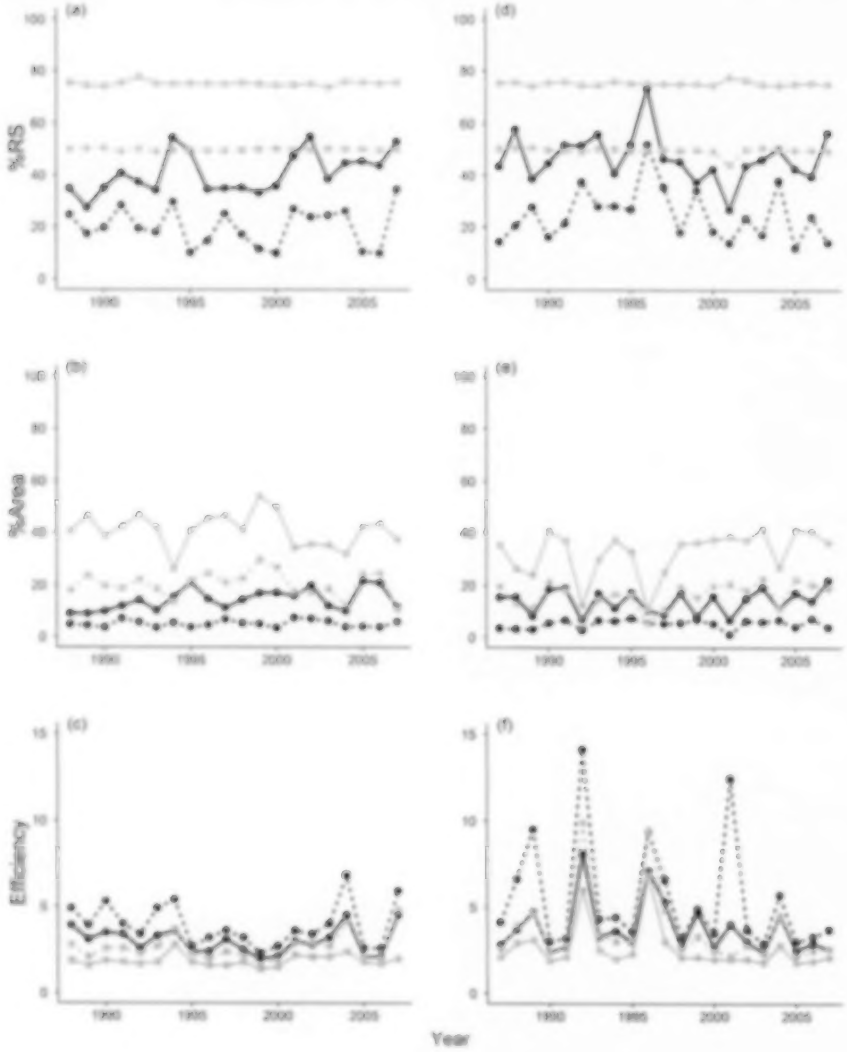


Fig. 3. (*a*, *d*) Percentage of juvenile red snapper abundance (%RS), (*b*, *e*) percentage of total area (%Area), and (*c*, *f*) efficiency inside the annual hot spots by intensity level for fall (*a*, *b*, *c*) and summer (*d*, *e*, *f*) by year. Efficiency is the ratio of %RS to %Area. Intensity levels are as follows: very high intensity (black broken line); high intensity (black continuous line); 50A (shaded broken line); 75A (shaded continuous line).



Conservation goals

Because of the trade-offs between intensity and persistence, the conservation goals could be met in different ways. To reach the goal of encompassing a minimum of 25% of the red snapper inside a marine reserve in fall, any of the following templates could be chosen: the template with very high intensity level and 2 years of persistence; the high intensity template with 4 years of persistence; the 50A intensity template with 6 years of persistence; or the 75A template with 9 years of persistence (Table 2). The composite hot spots that made up the templates for each of these alternatives in fall were of different shapes and in different locations, but the alternatives were similar in that very few of the composite hot spots were located off western Louisiana (Figs. 7*a*–7*d*). In summer, the template designated by the very high intensity level with a persistence of 2 years, the high intensity template with 4 years of persistence, the 50A intensity template with 4 years of persistence, or the 75A intensity template with 9 years of persistence would each reach the goal of at least 25% red snapper inside the marine reserve (Table 2). The alternative templates to reach the 25% red snapper goal in summer were very similar to each other, with one primary composite hot spot located off the Louisiana–Texas border (Figs. 7*e*–7*h*). The percentage of the total area required for meeting the 25% red snapper goal averaged about 18% over all templates in fall and 19% in summer, with average efficiency ratings of 1.7 in fall and 1.5 in summer.

Fig. 4. Composite map illustrating differences in persistence levels within the same intensity level (50A red snapper, the green area in Fig. 5) during (*a*) fall and (*b*) summer. Persistence levels are out of a possible maximum of 13 years in fall and 14 years in summer and are as shown in the key in *b* for both *a* and *b*. Only persistence levels ≥5 years are shown. Depth contours for 10, 20, 30, 50, 75, and 100 m are displayed. The Texas Closure (closure to commercial shrimping from May to July) is shown by the dashed–dotted line in summer. The hot spots with higher persistence are shown on top of hot spots with lower persistence due to their smaller spatial area.

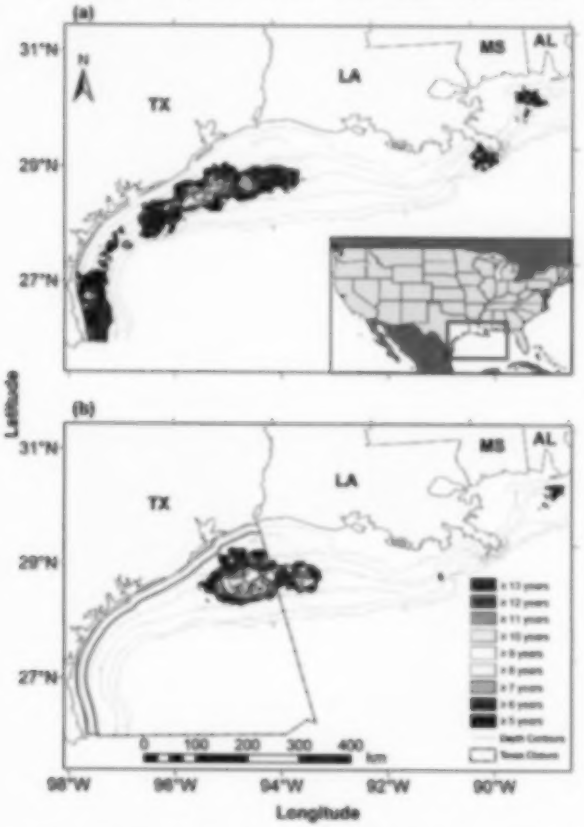
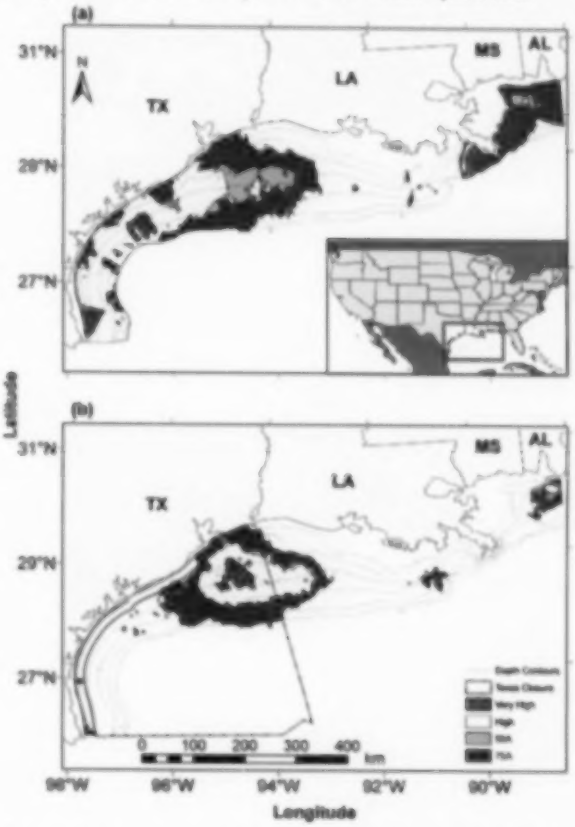


Fig. 5. Composite map illustrating differences in intensity levels within the same persistence level (≥5 years of persistence) during (*a*) fall and (*b*) summer. Intensity levels for both *a* and *b* are as shown in the key in *b*. Depth contours for 10, 20, 30, 50, 75, and 100 m are displayed. The Texas Closure (closure to commercial shrimping from May to July) is shown by the dashed–dotted line in summer. The hot spots with higher intensity are shown on top of hot spots with lower intensity due to their smaller spatial area.



To reach the goal of selecting a maximum reserve size of 15% of the total area as a management target, managers could choose the very high intensity template with 3 years of persistence, the high intensity template with 5 years of persistence, the 50A intensity with 6 years of persistence, or the 75A intensity with 10 years of persistence in fall. The same combinations of intensity and persistence could also be chosen in summer (Table 2). The average %RS in these templates was 18% in fall and 20% in summer, with average efficiency ratings of 1.8 in fall and 1.6 in summer.

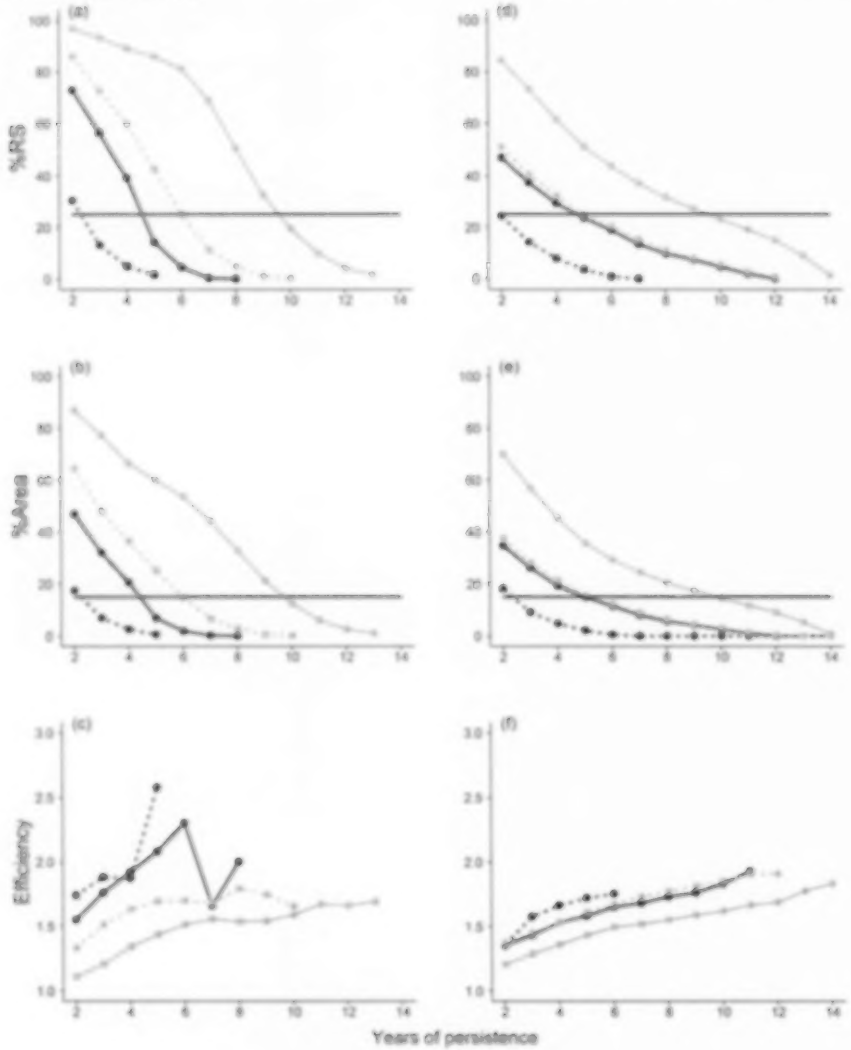
Discussion

Marine reserves for mobile species

Although the early literature was very optimistic concerning the effectiveness of marine reserves in meeting objectives ranging from protecting species diversity to increasing fisheries yield, scientists in recent years have recognized that marine reserves are just one of many tools available to meet conservation objectives (Allison et al. 1998). Marine reserves alone may not be sufficient to meet all management objectives and other strategies may be more effective for meeting particular goals, especially for mobile species (Hilborn et al. 2004). In this paper, we do not take sides on whether marine reserves are the best strategy for preserving mobile species or reducing bycatch. Instead, we investigate whether reserves can be a viable approach for reducing bycatch of mobile species and demonstrate how to choose the most efficient reserve based on the intensity and persistence of hot spots. Our results showed that it is possible to create marine reserves for at least some mobile species and to meet reserve objectives in terms of protecting a desired proportion of a population over time.

The main benefit of using the approach illustrated here is that different potential reserves can easily be compared, so that reserves can be chosen to provide the largest benefits to the bycatch species while minimizing the spatial extent of the closure, thus minimizing the impact on the directed

Fig. 6. (*a*, *d*) Percentage of red snapper abundance (%RS), (*b*, *e*) percentage of total area (%Area), and (*c*, *f*) efficiency inside the templates for marine reserves by intensity level and years of persistence for (*a*, *b*, *c*) fall and (*d*, *e*, *f*) summer. Area of the template was based on data from 1988 (fall) or 1987 (summer) through 2000, whereas %RS was based on data from 2001 to 2007. Efficiency is the ratio of %RS to %Area. Intensity levels are as follows: very high intensity (black broken line); high intensity (black continuous line); 50A (shaded broken line); 75A (shaded continuous line). The horizontal lines show the conservation goals of encompassing at least 25% of the red snapper (*a*, *d*) or 15% of the area (*b*, *e*) within the reserve.



fishery. In addition, although it is beyond the scope of the present work, the same approach could be used to determine the probability of catching the target species in any potential reserve, thus incorporating an economic dimension into the decision-making process. This method could also be used to incorporate spatially referenced effort data, so that the amount of bycatch reduction could be estimated with any particular reserve.

In conducting this study on juvenile red snapper, we found some general principles that may apply to other mobile species. First, as we initially hypothesized, there is a basic trade-off for juvenile red snapper between the intensity of hot spots and their persistence that is linked to spatial area. Specifically, higher intensity leads to lower persistence because higher intensity hot spots encompass a smaller area, which means that the hot spots have a lower probability of occurring in the same location over time. The characteristics of intensity and persistence are not artificial qualities created by the methods we used. Instead, they are related to the biology of the species and to the fundamental environmental and physiological parameters that effect its spatial distribution, in terms of both dispersion (the pattern of distances between individuals) and habitat preferences that influence the occurrence of individuals at a particular location. Because

Table 2. Alternative combinations of intensity and persistence for meeting conservation goals. Alternative combinations were chosen to approach conservation goals as closely as possible without exceeding the set limitations. A longer time series of data would allow refinement of the alternatives to more closely match the conservation goals.

Goal: ≥25% red snapper in marine reserve template					Goal: ≤15% total area in marine reserve template				
Intensity level	Persistence (years)	%RS	%Area	Efficiency	Intensity level	Persistence (years)	%RS	%Area	Efficiency
Fall									
Very high	2	30.5	17.5	1.7	Very high	3	13.0	6.9	1.9
High	4	39.3	20.6	1.9	High	5	14.1	6.8	2.1
50A	6	25.2	14.8	1.7	50A	6	25.2	14.8	1.7
75A	9	32.7	21.3	1.5	75A	10	19.6	12.4	1.6
Summer									
Very high	2	24.4	18.0	1.4	Very high	3	14.2	9.0	1.6
High	4	29.4	19.2	1.5	High	5	23.6	14.9	1.6
50A	4	32.3	21.2	1.5	50A	6	20.4	12.3	1.7
75A	9	27.3	17.3	1.6	75A	10	23.2	14.4	1.6

Note: Intensity level, the concentration of organisms in an area: very high, red snapper abundance ≥2 standard deviations (SD) above the mean annual abundance; high, red snapper abundance ≥1 SD above the mean annual abundance; 50A, area with highest abundance that summed to 50% of the annual red snapper abundance; 75A, area with highest abundance that summed to 75% of the annual red snapper abundance. Persistence, the number of years out of the time series (13 years in fall, 14 years in summer) that the annual hot spots occurred in the same location. %RS, the percentage of the total abundance of red snapper that would be encompassed by the marine reserve template. %Area, the percentage of the survey area (Mexican border to the Alabama–Florida border) encompassed by the marine reserve template. Efficiency, the ratio of %RS to %Area.

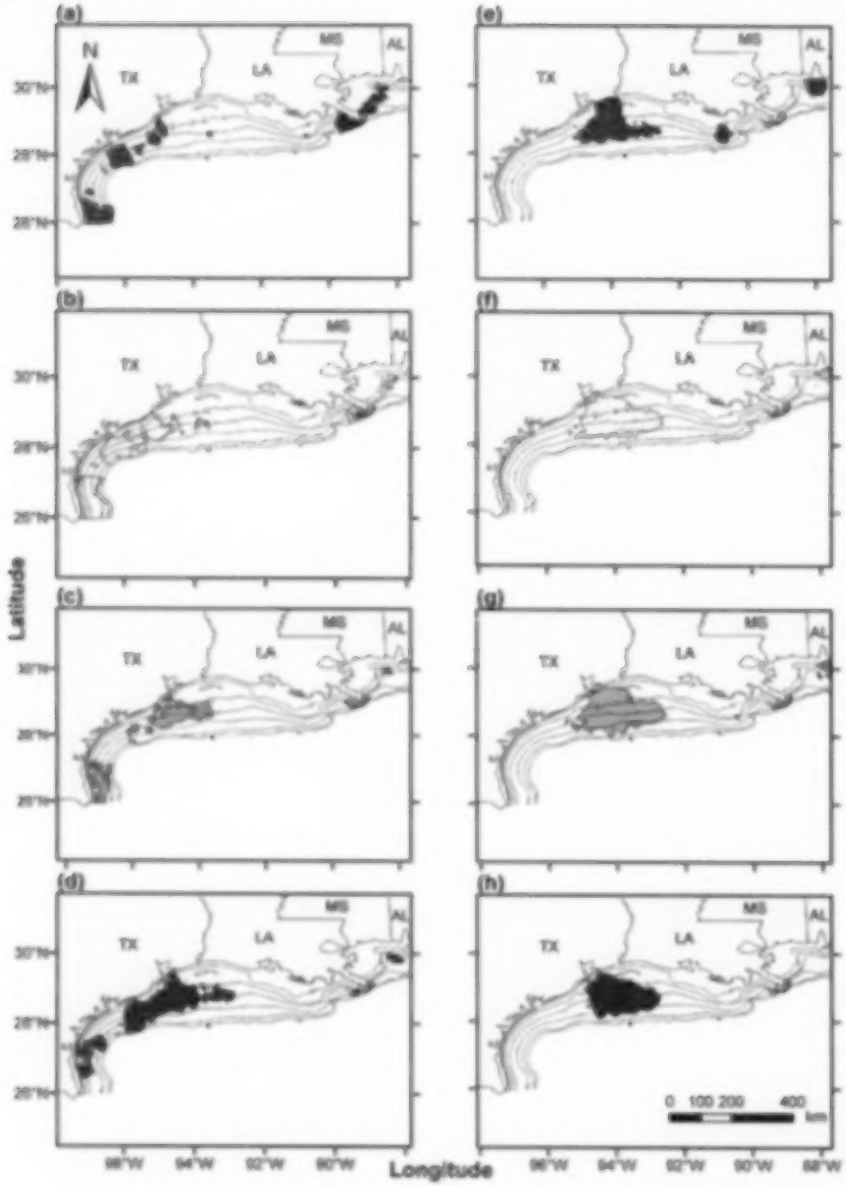
intensity and persistence are linked to biological attributes, the exact relationship between them will differ with different species. However, the trade-off will likely occur for any species that is not dependent on fixed habitat features, and it can be quantified for any species provided that there is a time series of spatially referenced abundance data. Second, achieving the desired level of protection can be accomplished by selecting different combinations of intensity and persistence. Fishery managers may decide that predictability is a more important feature than efficiency or that they are limited to a small area for consideration of a closure, making intensity more important. In any event, use of this approach will provide a foundation for making an informed decision on the design and placement of reserves, rather than making an ad hoc decision. Third, the desired level of protection may not occur every year, depending on how variable the locations of annual hot spots are from year to year compared with the location of the composite hot spot. Because the future is not always accurately predicted by the past, managers should continually evaluate the level of protection achieved and reconsider the location and size of marine reserves if the desired objectives are not achieved over time. Fourth, the nature of mobile species means that permanent year-round marine reserves may not be suitable for some species. For example, we found differences in hot-spot locations between seasons and some cyclical patterns in the spatial extent of hot spots that were likely due to shifts in the environmental parameters that are important in habitat choice. Thus, the use of seasonal reserves or transient reserves may be more appropriate, depending on the species, the management objectives, the temporal and spatial resolution of the data collected, and any trends over time that are discovered in the location or spatial extent of the annual hot spots. Real-time marine reserves may be the best option for reducing bycatch for some species. Real-time reserves are immediate closures of high bycatch areas, as illustrated by the Sea State program used in Alaska (Gilman et al. 2006). In this program, fishermen report bycatch rates by location while fishing. Data from the fleet are compiled immediately and information is relayed back to fishermen in high bycatch areas, prompting them to move to lower bycatch areas. The success of a program such as this would depend on how clustered the bycatch species is in space, the ability of fishermen to send and receive information while at sea, and the level of cooperation shown by the fishermen. It is possible that with increased incentives for fishermen to reduce bycatch and continued improvements in communications and location technology such as satellite-based vessel-monitoring systems, real-time marine reserves could be an option to reduce bycatch of mobile species, including bycatch of juvenile red snapper in the GOM shrimp trawl fishery.

Red snapper bycatch

Our results indicated that marine reserves could be an effective management strategy for reducing the bycatch of juvenile red snapper in GOM shrimp trawls. The efficiency ratings of the annual hot spots showed that there is an average of two to four times more red snapper inside the annual hot spots than in the surrounding area each fall and three to five times more each summer. The average efficiency ratings for the marine reserve templates showed that there are about 1.4 to 2.0 times more red snapper inside potential marine reserves than outside, and the persistence levels showed that these levels are predictable over time. Thus, even if total fishing effort remained constant but was simply redistributed into non-reserve areas, red snapper bycatch would be reduced by a larger amount using these potential reserves than by using randomly placed closures.

The use of marine reserves to reduce red snapper bycatch in GOM shrimp trawls was first mentioned in 1999 (Gulf of Mexico Fishery Management Council 1999), although no

Fig. 7. Maps of marine reserve templates for (*a*–*d*) fall and (*e*–*h*) summer illustrating the alternative combinations of intensity and persistence that can be used to achieve the conservation goal of encompassing a minimum of 25% of red snapper abundance within the reserve: (*a* and *e*) very high intensity with 2 years of persistence; (*b* and *f*) high intensity with 4 years of persistence; (*c* and *g*) 50A intensity with 6 and 4 years of persistence, respectively; and (*d* and *h*) 75A intensity with 9 years of persistence. The alternative templates for the conservation goal of reserving a maximum of 15% of the total area are not illustrated but were similar to the ones shown here. Shaded lines represent the 10, 20, 30, 50, 75, and 100 m depth contours.



specifics were provided as to how these reserves might be implemented. Throughout the 1990s, it was expected that bycatch reduction devices (BRDs; gear modifications to allow the escapement of fish from shrimp trawls) would reduce bycatch of red snapper enough that reserves would not be necessary (Reef Fish Stock Assessment Panel 1999). However, based on observations of the shrimp fleet from 2001 to 2003, BRDs were found to reduce red snapper bycatch by only 11.7% (Foster and Scott-Denton 2004). Because bycatch mortality in the shrimp fishery and overfishing in the directed fisheries continued unabated, 2007 management targets required a reduction in red snapper bycatch of 74% over the 2001–2003 baseline level to stop or reverse red snapper declines. In 2008, the use of time and area closures in the shrimp trawl fishery was written into the US regulations (Federal Register 2008). No details were provided; rather, the rule stated that a procedure would be established if necessary for implementing seasonal closures between depths of 18 and 55 m in the GOM if bycatch reduction targets were not met. Reductions in shrimp effort due to weather and market forces were sufficient to meet bycatch reduction targets in 2008 and 2009, so no closures were required.

Unfortunately, the area of a marine reserve required for a 74% reduction in bycatch mortality by the shrimp fleet is difficult to estimate without very fine scale fishing effort data from the commercial shrimp trawl fishery. The SEAMAP data used here are from a fishery-independent survey conducted by scientists, so fishing effort is well documented and the measure of abundance is the CPUE, or the catch rate of juvenile red snapper if fishing effort is equal at all locations. To translate from CPUE from the SEAMAP data to the total amount of bycatch in the shrimp trawl fishery, the amount of fishing effort conducted by the shrimp fleet, stratified by location, must be known. Fleet fishing effort is estimated by NMFS using port interviews with shrimpers as described in Nance (2004), but the data have very poor temporal and spatial resolution. The effort data have also been shown to be biased in both the amount and the spatial distribution of effort (Gallaway et al. 2003*a*). However, the recent use of electronic logbooks and vessel-monitoring systems has improved the accuracy and resolution of the effort data and should allow for this type of analysis in the future (Gallaway et al. 2003*b*).

Annual hot spots were spread along the entire Texas coastline (western Gulf coast) during the fall and clustered around the Texas–Louisiana border (central Gulf coast) in the summer. In general, the annual hot spots in the fall were larger and more diffuse than the annual hot spots in the summer. The widespread nature of the annual hot spots in fall likely reflects the location of spawning grounds or currents that deliver larvae to these areas, the availability of habitat, and water conditions that are within the temperature and oxygen preferences for red snapper. The location of summer hot spots off Texas may be partially explained by the Texas Closure and fish avoidance of the hypoxic zone. The Texas Closure, which has been in place since 1981, prohibits commercial shrimp trawling from May to July (45–60 days) in the offshore waters of Texas to allow brown shrimp to attain a certain size before harvesting. Because the summer SEAMAP survey generally takes place during the Texas Closure, the higher abundance of juvenile red snapper found off Texas in the summer may be due to the protection from bycatch mortality caused by the Texas Closure, while shrimping has continued to take place in the rest of the GOM. The hypoxic zone is an area of low oxygen (<2 $mg \cdot L^{-1}$) that forms each summer off western Louisiana. The hypoxic zone is caused by the decomposition of algae that bloomed because of the excess nutrients carried into the GOM by the Mississippi River. Because the hypoxic zone primarily extends westward from the Mississippi delta, red snapper trying to avoid the hypoxic zone may move to Texas waters. The lack of hot spots off south Texas in summer may reflect a lack of suitable habitat or water temperatures outside the preferred range for juvenile red snapper.

The locations of the annual hot spots varied both between seasons within a year and interannually by season. These differences in location are due to the physical, biological, and anthropogenic factors that affect the distribution of fish. Changes in location of the annual hot spots between seasons are due to the fact that the fall survey catches mostly age-0 fish, whereas the summer survey catches mostly age-1 fish. Therefore, differences in location between seasons reflect ontogenetic shifts in habitat preferences between age-0 and age-1 fish, as age-1 fish prefer larger structures than younger fish (Workman et al. 2002). Changes in the location of annual hot spots within the same season likely reflect differences in transient water conditions, spawning grounds, or larval supply. Although juvenile red snapper show preferences for water temperatures of 24–26 °C and dissolved oxygen of at least 5 $mg \cdot L^{-1}$ (Gallaway et al. 1999), these habitat parameters are widespread across the GOM and do not appear to explain the changes in location of the annual hot spots (S. Diamond, unpublished data). However, annual differences in the extent of the summer hypoxic zone may cause interannual movements of the summer hot spots as the extent of the hypoxic zone changes annually based on rainfall, and fish are known to shift to areas of higher oxygen to avoid hypoxia (Craig and Crowder 2005). Other factors such as currents, cold fronts, or storms that take place at local or regional spatial scales may also explain the interannual spatial variability in the location of the annual hot spots.

Uncertainties and caveats

The approach used here for placement of marine reserves has three main sources of uncertainty. Although we discuss these sources of uncertainty in terms of red snapper, they would apply to the data used for any species. First, the true abundance of organisms at each station is not a known value, but a sample with associated error. Although kriging accounts for this source of variability by allowing the nugget (*y* intercept of the semivariogram) to be set to a value larger than zero, this source of error was not specifically quantified in our study because tows at a single station were not replicated. Because variability of abundance at a single station is typically high for species associated with penaeid shrimp, it is likely that multiple replicate tows taken over multiple replicate days would be needed to reduce the standard errors to reasonable levels (Kennelly et al. 1993). The effect of high station-level uncertainty is that there is less smoothing of the

boundaries of the annual hot spots and reductions in both the %RS and the %Area in the annual hot spots at all intensity levels, leading to smaller composite hot spots and lowered persistence.

Second, we have used annual maps that are statistical estimates of the actual abundance and distribution of juvenile red snapper and overlaid them, creating a composite map with unquantified error. However, it may be possible in future studies to calculate confidence intervals around each annual map and then use the persistence levels to obtain a probability estimate for the composite maps, given the distributions of the annual maps. We are currently working to explore these possibilities.

Third, there is error associated with the methods of spatial interpolation. The choice of spatial interpolation methods can have a large impact on where hot spots are located and how much they overlap (S. Diamond and Y. Wang, unpublished data). The best interpolation method for any data set is dependent on the distribution of the organisms themselves, which differs among species and may differ among years within a species, making the choice of interpolation method difficult. In addition, unless the maps created by various interpolation methods can be ground-truthed, the choice of interpolation method will remain a source of unquantifiable error. Currently, we are attempting to address this source of uncertainty with an independent field-based study using side-scan sonar surveys in conjunction with shrimp trawling both inside and outside the hot spots defined by this research. The goals of the field study are to address whether small-scale abundance is predictable by large-scale, low-resolution data, to look for habitat features that might explain persistent hot spots, and to increase the confidence in potential closure areas based on spatial analysis of large-scale data.

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PERSPECTIVE / PERSPECTIVE

Incorporating lakes within the river discontinuum: longitudinal changes in ecological characteristics in stream–lake networks

Nicholas E. Jones

Abstract: Lakes and rivers are intimately connected in an alternating series of lentic and lotic reaches in many regions. The study of lakes and their outlets in hierarchical and branching river networks has not gained the attention of stream ecologists, and little effort has been focused on synthesizing the ecology of lake–stream interactions within a drainage network. Rapid and predictable changes in the ecological characteristics of streams occur at the interface with lakes. The influence that a lake might have on a stream is dependent on its position within the stream, stream type and size, lake size and shape, and the inlet and outlet positions. Little is known about the influences of multiple lakes within stream–lake networks and how these influences are determined by network shape and pattern. Fruitful collaborations and novel insights will come from the combined efforts of limnologists, stream ecologists, and landscape ecologists. Geographic information systems and network analyses will play an important role in summarizing aquatic landscape characteristics and creating a predictive science of aquatic networks. Lakes need to be more explicitly incorporated into ecological concepts in stream ecology, and reciprocally, streams need to be incorporated into ecological concepts involving lakes for the successful management and conservation of our aquatic resources.

Résumé : Dans plusieurs régions, les lacs et les rivières sont intimement reliés par une succession en alternance de sections lentiques et lotiques. L'étude des lacs et de leurs émissaires dans les réseaux fluviaux hiérarchiques et ramifiés n'a pas suscité l'intérêt des écologistes des eaux courantes et peu d'efforts ont été déployés pour faire la synthèse des interactions entre les lacs et les cours d'eau dans un même bassin versant. Il se produit des changements rapides et prévisibles dans les caractéristiques écologiques des cours d'eau à la rencontre des lacs. L'influence que peut avoir un lac sur un cours d'eau dépend de sa position dans le cours d'eau, du type et de la taille du cours d'eau, de la taille et de la forme du lac et de la position du tributaire et de l'émissaire. On sait peu de choses sur l'influence de lacs multiples dans les réseaux de lacs et de rivières et sur l'effet de la forme et de l'organisation du réseau sur ces influences. La combinaison des efforts de limnologistes, d'écologistes des eaux courantes et d'écologistes du paysage pourrait produire des collaborations intéressantes et ouvrir de nouvelles perspectives. Les systèmes d'information géographique et les analyses de réseaux joueront un rôle important en synthétisant les caractéristiques du paysage aquatique et en créant une science prédictive des réseaux aquatiques. Il est essentiel d'incorporer de manière plus explicite les lacs dans les concepts de l'écologie des eaux courantes et, réciproquement, les cours d'eau doivent être incorporés dans les concepts écologiques reliés aux lacs pour une gestion et une conservation réussies de nos ressources aquatiques.

[Traduit par la Rédaction]

Introduction

Stream ecologists typically see the landscape in terms of a network of streams that inevitably empty into another stream or lake, whereas limnologists typically see bodies of water dotted on the landscape. Stream ecologists have largely ignored stream networks punctuated with lakes. Similarly, limnologists have largely ignored streams connecting lakes (cf. Kling et al. 2000; Arp and Baker 2007; Marcarelli and Wurtsbaugh 2007). Soranno et al. (1999) examined spatial variation and ecological organization among lakes within chain lake systems across North America. They noted that although limnologists have long been interested in regional patterns in lake attributes, only recently have they considered lakes connected and organized across the landscape, rather than spatially independent entities (Martin and Soranno 2006). A similar perspective on the ecology of stream

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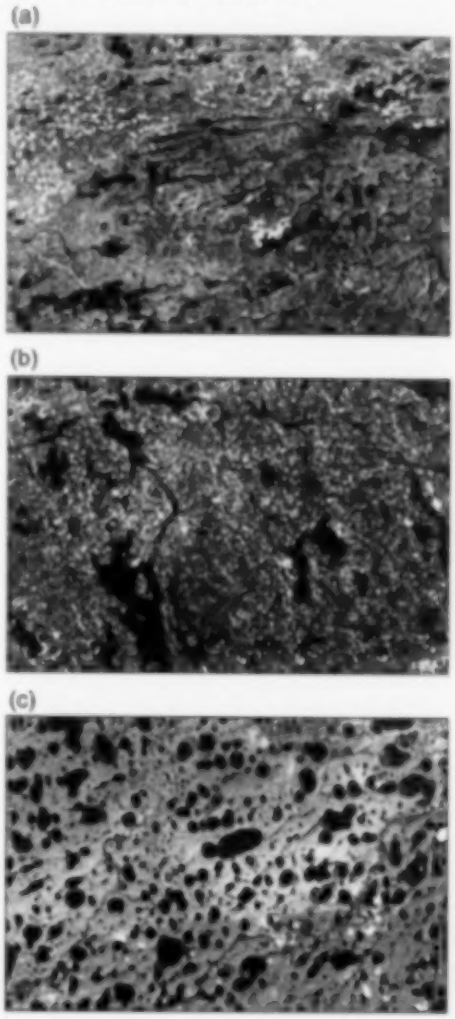
reaches connecting lakes in stream–lake networks has not been articulated.

Streams are typically envisioned as long channels of continuously moving water that drain watersheds, yet for many parts of the world (e.g., Canada, United States (US), Sweden, Finland, Norway, Russia, Argentina), streams and lakes are intimately connected (see Kratz and Frost 2000; Fig. 1). For example, the Canadian Shield occupies an area of 4.6 million km^2 or nearly half the land area of Canada and is densely populated with lakes and interconnecting streams (Fig. 1*a*). Portions of the Shield are also found in Minnesota, Wisconsin, Michigan, and New York. In Ontario, this Shield region has many lakes (35 000 lakes > 20 ha) and an even greater number of streams. For instance, the mainstem of the Petawawa River has 26 lakes on its 200 km length. In central Canada, the Churchill River has 52 large lakes on its 1300 km length and many unnamed lakes representing wider reaches of the river. In addition, ephemeral beaver (*Castor* spp.) ponds within watersheds are often not mapped. In Alaska, Canada, and Russia, streams flow through small shallow thaw lakes that are abundant in lowland ice-rich permafrost (Fig. 1*c*).

The river continuum concept (RCC; Vannote et al. 1980) provides a conceptual framework for understanding the fluvial system as an integrated series of physical gradients and associated biotic adjustments along the stream. This view of the river represents one of the most influential conceptual works in river ecology as evident in the many concepts it has spawned, many of which challenge this linear view (e.g., Rice et al. 2001; Poole 2002; Benda et al. 2004). More recently, stream ecologists have taken a view of the river that incorporates ideas from landscape ecology and the influence of tributaries to develop the hierarchical patch dynamics concept (Poole 2002) and network dynamic hypothesis (Benda et al. 2004). However, as Poole (2002) notes, the river discontinuum view does not dismiss the older continuum view so much as "subsume" it: gradual transitions between habitat patches do occur, resembling a continuum. Poole (2002) noted that the "river discontinuum" is comprised of hierarchically nested patches and individual stream segments arranged longitudinally in space, many of which might have unique and dynamic structures and functions over time. In this network view, the river is a population of channels and confluences, each of which generates unique streams. Benda et al. (2004) developed the network dynamics hypothesis, providing a structural basis for predicting how disturbances or watersheds interact with the spatial structure of river networks to generate spatial heterogeneity in habitat along river profiles and throughout watersheds. This view emphasizes variation rather than the average state in stream character and, thus, complements the concept of hierarchical patch dynamics.

Ward and Stanford (1983) advanced the serial discontinuity concept as a theoretical perspective of regulated rivers that predicts and explains the effect of reservoirs along the river continuum. In this linear perspective, reservoirs disrupt the continuum and cause upstream–downstream shifts in abiotic and biotic parameters and processes. The effect is related to the position of the dam along the continuum. For example, a bottom-draw dam in the lower reaches of a river may sharply decrease water temperature. Although there have been numerous studies on the influence of reservoirs on river structure and function, there has been much less investigation focused on the influence of natural lakes.

Fig. 1. Satellite imagery from 2007 of contrasting stream–lake networks found around the world (Google Maps, http://maps.google.ca/maps?hl=en&tab=wl): (*a*) a typical area of the Canadian Shield north of Thunder Bay, Ontario; (*b*) 60 km northeast of Helsinki, Finland, showing strong geologic control; and (*c*) thaw lake systems generating regular circular lakes on the North Slope of Alaska. Black areas and lines indicate water.



Despite the abundance of stream–lake networks, the ecology of streams connecting lakes and stream–lake networks taken together has been largely ignored (cf. Kling et al. 2000; Marcarelli and Wurtsbaugh 2007; Luecke and MacKinnon 2008). Hence, the available literature is limited for review. Concepts in stream ecology have advanced our understanding of streams for many areas of the world, yet a theoretical perspective synthesizing the ecology of stream–lake networks is lacking. The structure and ecology of stream–lake networks have important implications for the

way in which we view river ecosystems, thus influencing how we design studies, interpret data, and manage our natural resources.

In this synthesis, I begin by considering the local effects of a lake on a downstream stream segment. This initial discussion explores the influence of lake position in a watershed on the outcome of a lake's effect and takes a linear perspective for illustrative purposes. I then describe how characteristics of lakes and their inlet and outlet streams (size, shape, configuration, and serial juxtaposition of multiple lakes) might modify expected influences on downstream segments. In the second section of this paper, I explore the broader perspective of lakes within stream networks. This larger-scale whole-network perspective strives to incorporate the interactions among lakes and between lakes within contrasting network patterns. Lastly, I discuss lake effects on fish distribution and community structure in stream–lake networks. Lakeless streams are not discussed here because they should follow predictions of the river continuum concept or have variability not due to lakes. Other sources of variability creating discontinuities include confluence points (Benda et al. 2004), beavers (Collen and Gibson 2001), geology, land use, and anthropogenic factors, e.g., culverts, forestry, and hydropower.

Terminology

For the purposes of this synthesis, streams draining the landscape without lakes on their drainage network will be called lakeless streams (Hynes River before it enters Lake Vannote; Fig. 2), whereas lake-effect streams have one or more lakes on their drainage network (Hynes River downstream of Lake Vannote; Fig. 2). Overall, the collection of streams and lakes are called a stream–lake network or, sometimes, "chain lakes". An outlet stream (outlet A) drains Lake Vannote and becomes an inlet stream (inlet B) where it empties into Lake Stanford (Fig. 2). Stream segments between lakes are identified by the lake flowing into the stream and the lake receiving the stream, e.g., Vannote-Stanford segment of the Hynes River (Fig. 2). The influence of the upstream lake on the outlet stream is called the lake effect.

The influence of lakes on outlet streams: a linear perspective

Lakeless streams in forested regions may exhibit continuous downstream trends in energy inputs and habitat structure as predicted by the RCC (Vannote et al. 1980), but many will express a discontinuous pattern (Poole 2002). In headwater streams, we can expect that stream characteristics will be influenced by riparian vegetation that shades the stream and provides course particulate organic matter (CPOM) input. Here, heterotrophy will be more prevalent than autotrophy. Benthos belonging to the shredder and collector functional feeding groups and coolwater fishes that feed mainly on invertebrates will likely dominate. In midreaches, riparian vegetation has less influence on the wider stream. Sunlight now reaches more of the stream, and periphyton and macrophytes become the primary energy sources. Benthos dominance shifts from shredders to grazers, and fishes shift from coldwater to piscivorous, coolwater species. In lower reaches, increasing turbidity and depth cause the river

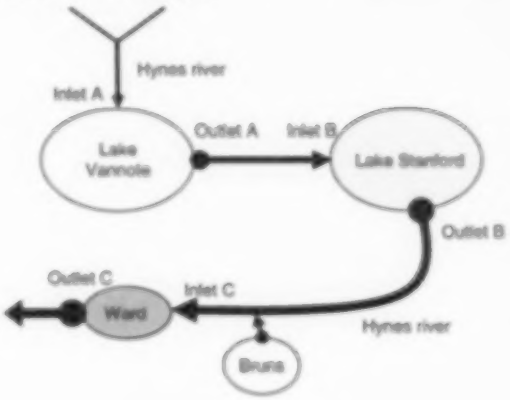


Fig. 2. Schematic representation of a stream–lake network illustrating some of the different configurations of lake size and location within a drainage area. Downstream ecological impacts of different lakes are illustrated in Fig. 5.

to become more heterotrophic, although phytoplankton and macrophytes will be present. Invertebrates that use fine particulate organic matter (FPOM) dominate the benthos. Warmwater and planktivorous species of fish may be present. Exceptions to these longitudinal gradients described in the RCC are many and include streams in biomes where tall riparian vegetation is absent (e.g., grasslands, desert, and the Arctic), regulated streams, and stream–lake networks, the focus of this paper.

Ward and Stanford (1983) hypothesized relationships among physical, chemical, and biological variables as functions of stream order (distance) along a stream continuum. They illustrated the influence that reservoirs can have on the continuum depending on their position (headwater, midreach, and lower reach) in the stream network. In this model, Ward and Stanford assume that a reservoir releases cold oxygenated hypolimnetic water during summer. Despite obvious differences between reservoirs and lakes, many of the relationships that they hypothesized for reservoirs may hold true for natural lakes. In the following section, relationships between stream order and various parameters were derived from key sources in the literature (e.g., Vannote et al. 1980; Ward and Stanford 1983; Naiman et al. 1987). The point of this discussion is to illustrate the influence of a lake located in the headwaters, midreaches, and lower reaches of a river. For the purpose of illustrating chain-lake systems, I do not consider other influences such as confluences or tributaries, which form the basis of the discontinuous view of rivers as described above (Poole 2002).

Lake effects on physical attributes of outlet streams

The storage capacity of lakes tend to stabilize the thermal and flow regime characteristics of outlet streams. During summer months, a lake will provide warm (Fig. 3*a*) epilimnetic water to the outlet stream (Wotton 1995; Dorava and Milner 2000; Luecke and MacKinnon 2008). In headwater streams, the lake effect decreases progressively downstream as warm, epilimnetic water cools in the presence of increased riparian shading and groundwater inputs. Some streams may not be able to shed added heat during the

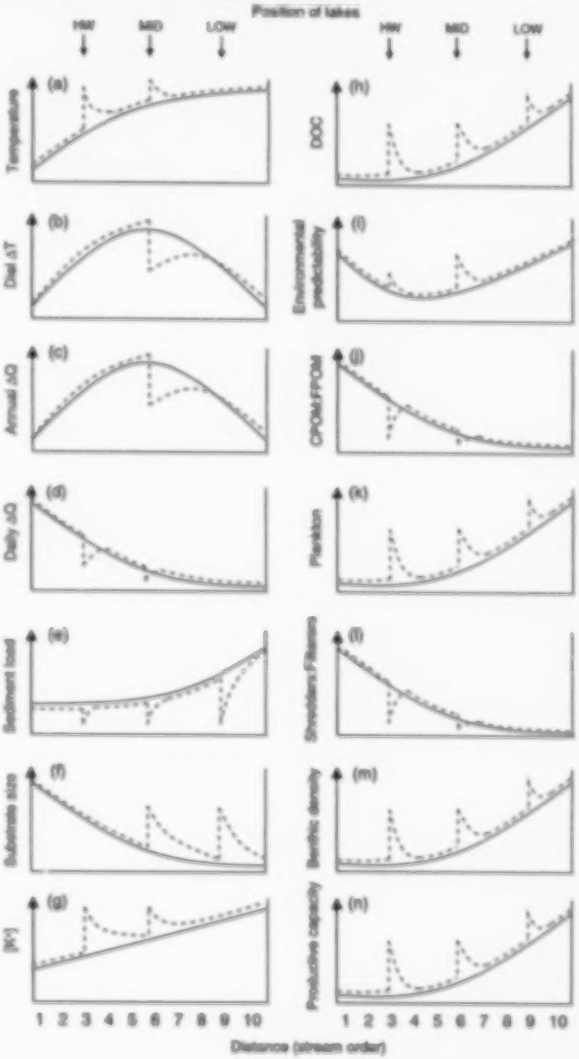
summer, and downstream water temperatures may continue to warm as a result of normal stream heating processes. As stream size increases, the influence of lakes on water temperatures will likely decrease (Fig. 3*a*) because larger streams are typically warmer already. Because of the large thermal inertia of lakes, these warmer temperatures may persist well into the fall season (Fukushima and Smoker 1997; Hieber et al. 2002; Luecke and MacKinnon 2008) but are cooler in the spring. During winter, ice formation and transport in the outlet stream may be reduced, resulting in less scouring and damage to biota and their filter-feeding structures.

The large thermal inertia of a lake also results in less diel variation in water temperatures (Fig. 3*b*) than would be observed in most lakeless streams except those with high inputs of groundwater (Hieber et al. 2002; Jones et al. 2003*a*; Luecke and MacKinnon 2008). Decreases of the diel range will be most dramatic below a lake in the middle reaches where the greatest daily thermal range is normally observed (Caissie 2006). Less diel variation and warm epilimnetic water temperature can result in more degree-days that increase rates of decomposition and nutrient turnover, stimulate the growth of primary and secondary producers (e.g., algae, benthic invertebrates, and fish), and enhance ecosystem productivity (Jones et al. 2003*a*; Dorava and Milner 2000). During the warm summer months, fishes may leave the outlet stream and move into the lake or downstream to cooler locations if the outlet temperature increases above their preferred temperature or water levels become exceedingly low.

The flow regime of an outlet stream will be partially dictated by water levels in the upstream lake. Lakeless streams flowing into a lake are influenced by the nature of the watersheds they drain and may vary from highly variable and unpredictable to very stable flow regimes (Poff and Ward 1989). Regardless of the flow characteristics of lakeless streams draining into a lake, the lake will dampen or moderate flow fluctuations (ΔQ; Figs. 3*c*, 3*d*) such that outlet flows may be sustained during periods of drought or freezing (Dorava and Milner 2000; Arp et al. 2006). The damping effect of lakes on the runoff hydrograph can prevent small runoff events from maintaining a measurable flood wave through the basin (Spence 2006). The location at which a runoff event is interrupted in the watercourse is a function of lake size relative to upstream runoff inputs. Runoff is more susceptible to evaporative losses in large receiving lakes where inflow per unit area is less. These processes may cause intermittent streamflow in small outlets (Spence 2006).

The sediment load (Fig. 3*e*) in outlet streams is generally low because most sediment in inlet streams will settle out before reaching the outlet stream (sediment sink; Dorava and Milner 2000; Arp et al. 2007). If the continuity of sediment transport is interrupted by lakes, the flow in the outlet may become sediment-starved (Kondolf 1997) and prone to erode the streambed and banks, producing channel incision (down-cutting), coarsening of bed material (often called armouring; Myers et al. 2007; Luecke and MacKinnon 2008), and loss of spawning gravels (as smaller gravels are transported without replacement). Bed sediments in lake outlet segments are likely less mobile during bankfull flows in contrast to sediments at lake inlets (Myers et al. 2007). The coarsening of substrate (Fig. 3*f*) will be less pronounced in headwater streams where substrate sizes are generally large, whereas in lower reaches, fine substrate may be removed. In a mountain lake district, Arp et al. (2007) noted 50% recovery of sediment characteristics 1–5 km downstream, but for some streams, full recovery required 10–20 km. Outlets are

Fig. 3. Relative changes in physical and chemical variables as a function of stream order in lakeless streams (continuous lines; based on Vannote et al. 1980; Ward and Stanford 1983; Naiman et al. 1987). The postulated effects of lakes in forested headwaters (HW), midreaches (MID), and lower reaches (LOW) of a river are illustrated with broken lines (modified from Ward and Stanford 1983). Lakes are illustrated as points for simplicity, and the influences of other factors (e.g., tributaries) along the discontinuum are ignored. ΔT, temperature change; ΔQ, change in flow; DOC, dissolved organic carbon; CPOM, coarse particulate organic matter; FPOM, fine particulate organic matter.



typically wide and shallow with coarse sediment, whereas inlets are narrow and deep with finer sediment (Arp et al. 2007; N.E. Jones, personal observation). In contrast, Dorava and Milner (2000) found that lakes lead to narrower channels, more stable banks and riparian areas, and more diverse and stable habitat in contrast to glacial streams (braided, anastomosing streams) without lakes. This difference suggests that the response of the outlet stream may be predictable if the context, i.e., catchment and sediment characteristics, are considered (Montgomery 1999). Dorava and Milner (2000) also observed that lakes reduced suspended sediment dramatically in glacier-fed systems in Alaska.

Lake effects on chemical attributes of outlet streams

There is surprisingly little information in the literature concerning longitudinal changes in water chemistry in lake outlet streams (but see Kling et al. 2000; Arp and Baker 2007). In general, the similarity in chemical characteristics between lake surface waters and outlet streams will decrease with distance downstream. Tributary streams and groundwater may deliver water of contrasting chemical composition that alters water chemistry in the outlet stream (Bruns et al. 1984). Kling et al. (2000) noted that streams tend to have higher concentrations of major anions and cations than lakes within the same network, which had higher concentrations of particulate carbon, nitrogen, phosphorus, and chlorophyll *a*. Kling et al. (2000) observed predictable differences in water quality parameters measured at the inlet versus the outlet of lakes and in parameters measured at upstream versus downstream sites in the stream-reach connecting lakes. In-lake processing tended to consume alkalinity, conductivity, H^+, dissolved inorganic carbon (DIC), Ca^{2+}, Mg^{2+}, CO_2, CH_4, and NO_3^-, and produce K^+ and dissolved organic carbon (DOC). In-stream processing resulted in the opposite trends (consumption of K^+ and DOC; Figs. 3*g* and 3*h*), and the magnitudes of change were often similar to those measured in the lakes but with the opposite sign (Kling et al. 2000). Arp and Baker (2007) found that there was very little nitrate uptake in most lake outlet streams, whereas PO_4^{-3} uptake was higher at outlets in comparison with reference and lake inlet reaches. They also noted that the best predictor of patterns in nutrient demand was the proportion (%) of watershed area not routing through a lake. They estimated that NO_3 and PO_4^{-3} uptake returned to 50% of above-lake conditions within 1–4 km downstream of a small headwater lake but required considerably greater distances for larger lakes positioned lower in the watershed.

Lake effects on biological characteristics of outlet streams

Combined changes in the thermal, flow, and sediment regimes observed at lake outlets creates an environment or habitat template (sensu Southwood 1988) that is less variable or harsh (Fig. 3*i*) than lakeless streams (Dorava and Milner 2000; Hieber et al. 2002; Jones et al. 2003*a*). In this environment, species with life histories more suited to low variability environments will be favoured over those with life histories suited to environmental instability. Stable flow regimes and low amounts of sediment moderate the disturbance regime in the outlet stream (see Wootton et al. 1996; Myers et al. 2007), likely reducing the magnitude of periphyton scour following spates and perhaps allowing a greater accrual of biofilm and mosses that provide food and habitat for benthic invertebrates and, subsequently, fishes (Haraldstad et al. 1987; Dorava and Milner 2000). The influence of a lake will decrease downstream to a point where stream attributes resemble lakeless streams, thereby increasing the diversity of habitat types within the watershed as a whole.

Organic matter

Lakes act as transducers along the river network that alter the quantity and quality of organic matter delivered to stream reaches. A lake may supply an outlet stream with a rich source of organic carbon ranging from dissolved to CPOM (Fig. 3*j*), including course woody debris (Kownacki et al. 1997). Richardson and Mackay (1991) noted that large aggregations of filter-feeding invertebrates, each with a particular particle size preference (Harding 1997), will selectively ingest particles that are more likely to enhance growth (high quality foods), reducing their availability downstream. The consumption of DOC by invertebrates may explain the in-stream decrease of DOC as noted by Kling et al. (2000). In turn, invertebrate fauna alter the DOC size spectrum and, thus, the assemblage of invertebrate species downstream (Wotton et al. 1998; Parkes et al. 2004). Vadeboncoeur (1994) observed that although initial concentrations of suspended organic carbon are determined by the lake within a short distance (<3 km), concentrations become regulated by in-stream processes (including sedimentation and consumption by filter-feeding invertebrates). In addition to the large amount of energy flowing into the outlet, outlet streams likely have higher proportions of phytoplankton providing a source of labile DOC as opposed to residual refractory carbon of terrestrial origin from similarly sized lakeless streams.

Plankton

Phytoplankton, zooplankton, and bacterioplankton are abundant in epilimnetic lake waters (Fig. 3*k*) delivered to the outlet (Haraldstad et al. 1987; Parkes et al. 2004) where dramatic changes occur within the biological community. The morphology of the littoral zone influences the transport of zooplankton into outlet streams (Walks and Cyr 2004). Once in the outlet stream, water velocity, depth, and likely width-to-depth ratios are the principle factors influencing particle transport downstream (Paul and Hall 2002; Walks and Cyr 2004). The extent of lake influence on seston density expands and contracts longitudinally with increases and decreases in discharge on any individual stream (Vadeboncoeur 1994; Campbell 2002). Vadeboncoeur (1994) found a longitudinal decrease in lake-derived phytoplankton that was balanced by an increase in stream algae. Drift in lake outlet streams is typically dominated (>90% by abundance) by planktonic microcrustaceans (Jones et al. 2003*b*) similar in species composition to upstream lakes (Campbell 2002). Depending on the habitat characteristics of the outlet stream (e.g., cascades and riffles), many of the fragile planktonic organisms may be damaged or killed by turbulent flows (Richardson and Mackay 1991). In the lower reaches of rivers, the abundance of planktonic organisms may be relatively high, so plankton-rich lakes may have relatively little influence in lower reaches (Fig. 3*k*).

Benthos

The high density of benthic invertebrates in lake outlet streams (particularly filter-feeding) and their rapid decline downstream has been attributed to gradients in food resources, flow, temperature, and sediment regimes. The high particulate density drifting into outlet streams provides vital energy and nutrients required for the growth of benthic invertebrates (Robinson and Minshall 1990) and mussels (Welker and Walz 1998). This energy transfer from one habitat to another subsidizes the outlet food web (Polis et al. 1997; Doi 2009); the food base for benthic invertebrates can be dominated by lacustrine inputs (>80%) in small shaded lake outlets (Junger and Planas 1994). Filter-feeding organisms (e.g., Simuliidae and Hydropsychidae) typically dominate the benthos of lake outlets (Fig. 3*l*) much like reservoir outlets (Ward and Stanford 1983; Wotton 1988). This filtering of particulate carbon can increase the retention of carbon and decrease nutrient spiralling length (Ensign and Doyle 2006). Dorava and Milner (2000) noted that benthic densities and diversity below Skilak Lake on the Kenai River system were about four times that found in the lakeless glacier-fed Johnson River some 100 km away. The density (Fig. 3*m*) and size of filter-feeding benthos typically decreases with downstream distance from a lake (for a review of mechanisms creating this gradient, see Richardson and Mackay 1991; McCreadie and Robertson 1998). Farther downstream, a large amount of particulate matter has either been filtered out by benthos or has settled to the streambed (Richardson and Mackay 1991; Wotton et al. 1995; McCreadie and Robertson 1998). This nutrient export can be traced downstream for 10 to 10 000 m, depending on the physical characteristics of the stream (see Plankton above).

Dissolved organic matter from lakes may be a significant food source for many benthic groups, including Trichoptera and Simuliidae larvae (Ciborowski et al. 1997). For example, Wotton et al. (1998) observed black fly densities greater than 60 000 individuals·m^{-2} in a lake outlet stream, suggesting that black fly larvae are "allogenic ecosystem engineers" capturing fine and dissolved organic matter from suspension. The egested fecal pellets are then available to the benthic microbial and invertebrate communities.

Fishes

Fishes inhabiting the outlet stream can benefit from the higher densities of benthos and zooplankton drift and higher water temperatures (Irvine and Northcote 1982; Hayes 1995; Jones et al. 2003*b*). Jones et al. (2003*a*) noted that differences in the characteristics of some Alaskan (mainly lakeless streams) and Barrenlands (mainly lake outlets) tundra streams propagate to higher trophic levels, increasing the capacity of outlet streams to support greater benthic invertebrate and fish production (Fig. 3*n*). In an assessment of the importance of small lakes, Irvine and Johnston (1992) determined that coho (*Oncorhynchus kisutch*) fry generally grew fastest in lakes and their outlet streams on Vancouver Island. Similarly, Dorava and Milner (2000) state that sustained summer flows, warmer water temperatures, suitable instream and riparian habitat, and stable coarse substrates led to enhanced salmon (*Oncorhynchus* spp.) productivity compared with purely glacier-fed systems. Luecke and MacKinnon (2008) also found that the growth of Arctic grayling (*Thymallus arcticus*) in a stream–lake network was 50% greater than in an adjacent lakeless stream network. Although several studies have shown that benthic densities are higher near the lake and decrease downstream (Richardson and Mackay 1991), published examples of this longitudinal gradient for fishes in terms of density, biomass, or growth are absent. Jonsson and Sandlund (1979), however, noted that brown trout (*Salmo trutta*) caught 10 km downstream from the outlet had growth comparable with trout from an inlet stream. The characteristics and properties of lake outlets, i.e., resource subsidy and benign environment, may promote higher productivity than would be observed in streams without lakes (Hieber et al. 2002; Jones et al. 2003*a*; Luecke and MacKinnon 2008). Such an understanding could lead to more refined estimates of river production and management of fishery resources (Gibson 2002). Randall et al. (1995) proposed that rivers are generally more productive for fish than lakes. In this review, we see that outlets, or at least the segments of streams near the lake outlet, are perhaps more productive than neighbouring lakeless stream systems.

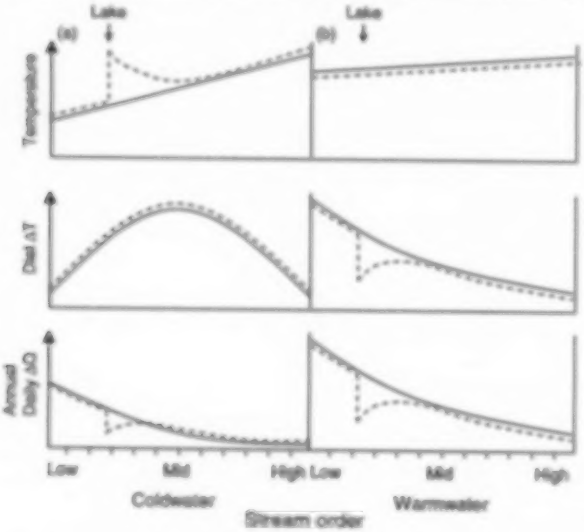
Landscape dependence of lake effects

Lake effects have a strong contextual basis that is influenced by the characteristics of a particular landscape (Montgomery 1999). For example, the effect of a lake on a flashy and turbid warmwater stream dominated by surface flow contrasts sharply with the effect of a lake on a coldwater trout stream. Coldwater streams in forested catchments of temperate latitudes often have groundwater inputs resulting in relatively constant water temperatures and flows, whereas warmwater streams often lack groundwater and (or) surrounding forests resulting in large diel variation in water temperature and variable, perhaps intermittent, flows (Fig. 4). Upon entering a lake, shading is absent and water temperature rises dramatically in the formerly coldwater stream. As a result, the coldwater stream is transformed into a warmwater stream by receiving warm epilimnetic water; however, diel temperature and flow variability remain relatively unchanged and low (Fig. 4*a*). In contrast, water temperatures in the warmwater stream are less variable: flow and diel temperature variability are reduced and perennial base flow may be observed (Fig. 4*b*). Further downstream, the lake effect diminishes even more and the continuum is re-established or perhaps altered by joining a large, contrasting river type (Benda et al. 2004).

Lake size, lake shape, stream size, and inlet and outlet position

The physical, chemical, and biological characteristics of outlet streams are determined, in part, by the characteristics of the source lake and the streams that flow into it. Within a lake, inflowing materials are captured, processed, transformed, and released in the outlet water. The position of inlets and outlets may also determine the degree of lake influence. A lake with inlets and outlets at the opposite ends (Fig. 5*a*) will alter the inflowing stream to the greatest degree, whereas inlets and outlets in close proximity may short-circuit the lake effect, particularly during high flows (Fig. 5*b*). The latter might be particularly true if the tributary angle of entry into the lake points directly to the lake outlet.

Fig. 4. Context dependence of lake effects on three factors: stream temperature, diel stream temperature change (ΔT), and annual and daily variability in discharge (ΔQ) in (*a*) a coldwater stream vs. (*b*) a warmwater stream (modified from Ward and Stanford 1983). Position of the headwater lake is indicated by arrows. Continuous and broken lines represent lakeless and lake outlet streams, respectively.



The degree of influence that the lake has depends largely on the relative size of the stream and lake. For example, the characteristics of a small stream flowing into a large lake with a low flushing rate (Fig. 5*c*) have the potential to be significantly altered, whereas a larger river flowing into a small lake with a high flushing rate may retain many of its physical and chemical characteristics (Fig. 5*d*).

Lake residence time (days to years) is dependent on internal physical processes (Ambrosetti et al. 2003). Lake shape and the presence of islands will influence flow patterns, and simple calculations of inflow to lake volume are inadequate to assess the extent of water mixing. Depending on the water temperature of the stream relative to that of the lake, a stream may move through a lake in a variety of ways: as surface overflow, as intermediate depth interflow, or as near-bottom underflow. High flows at certain times of year influence when most of the mixing and outflow occurs; hence, there is seasonality in the mixing process. Circulation of the lake is further influenced by the Earth's rotation so that incoming rivers flow preferentially counter-clockwise along the shoreline of lakes in the northern hemisphere (Carmack et al. 1979).

Effects of multiple lakes along the river continuum

Ward and Stanford (1983) developed a conceptual model to quantify the linear effects of multiple reservoirs on the continuum. This view of a river shows the compound linear effect of multiple impoundments along a river, which are also manifest in natural lake chains. Reservoirs disrupt the continuum and cause upstream–downstream shifts in abiotic and biotic structure and function. In multiple-lake scenarios, the continuum may never match the characteristics of their lakeless stream relatives. For example, changes in ecological

Fig. 5. Effects of discharge and inlet stream configuration on lake effects. A lake with inlets and outlets at opposite ends (*a*) will provide a greater opportunity for transformation of ecological characteristics than if the inlet and outlet are very close (*b*). Similarly, lake effects will be greatest when discharge is low relative to lake volume (*c*) and less when the discharge is high relative to lake volume (*d*). Similarly, arrows indicate the direction and magnitude of river flow.

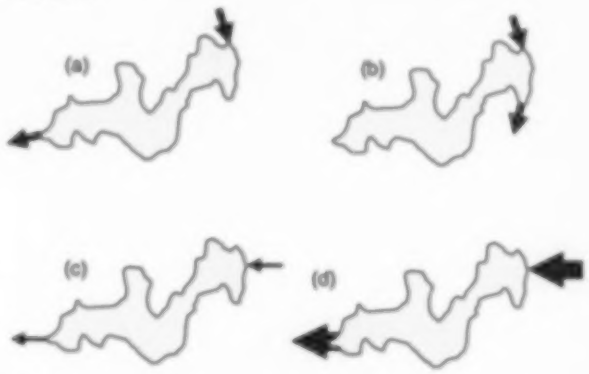
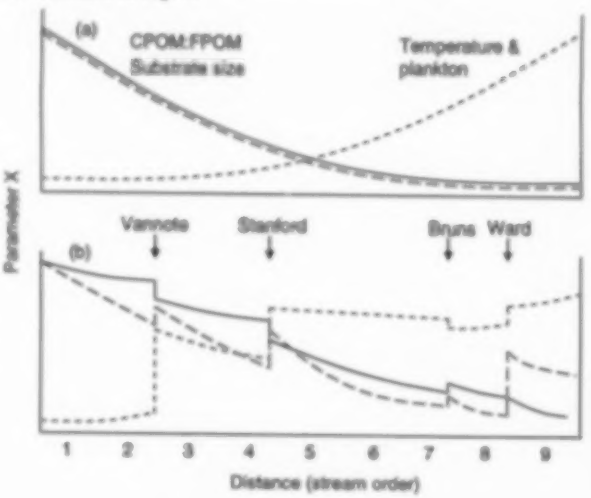


Fig. 6. Hypothesized changes in ecological characteristics of a forested stream as it flows through the stream–lake network represented in Fig. 2. (*a*) Relative changes in temperature and plankton (short-dashed line), ratio of coarse particulate organic matter (CPOM) to fine particulate organic matter (FPOM) (continuous line), and substrate size (long-dashed line) in a lakeless stream according to the river continuum concept (RCC; Vannote et al. 1980). (*b*) The hypothetical changes from lakes disrupting the continuum as illustrated in Fig. 2.



characteristics of a forested stream without lakes (Fig. 6*a*) can be very different from those of a stream with lakes that punctuate the continuum causing up- and down-shifts in expected condition (Fig. 6*b*). Below I expand on Ward and Stanford's linear perspective of lakes punctuating a continuum to develop the idea of a chain lake network including lakes distributed throughout river networks, which generate heterogeneity in river habitat characteristics at a landscape level.

Fig. 7. The influence of a lake is likely to decrease as rivers increase in size down the network.

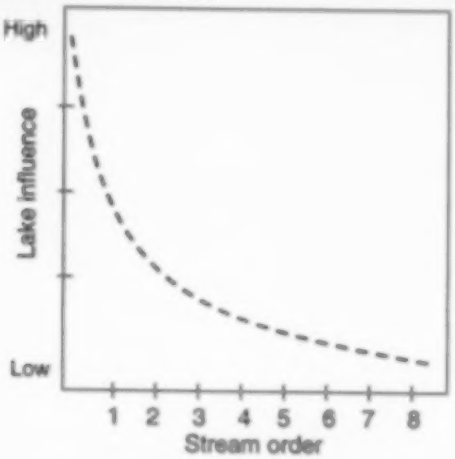
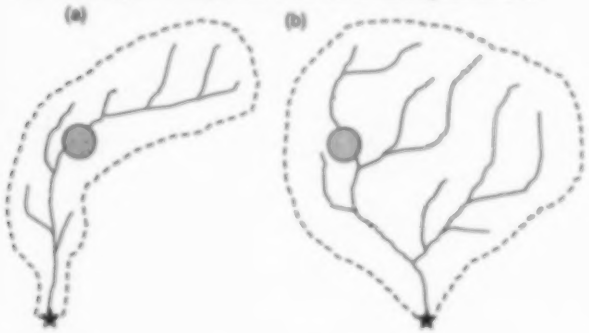


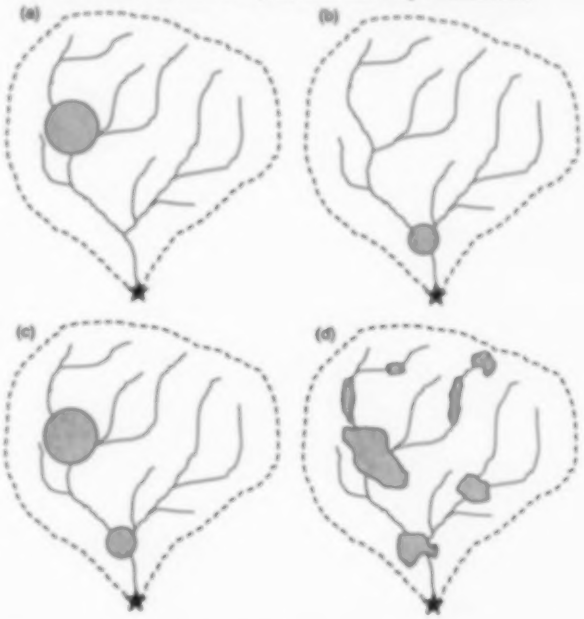
Fig. 8. (*a*) Trellis and (*b*) dendritic network drainage patterns and respective basin shapes illustrate how basin shape influences lake effects. A single lake in the midreaches of a trellis network may alter the ecological characteristics (e.g., flow regime) without dilution from large neighbouring network branches for many kilometres. In contrast, the same placement of a lake in the dendritic basin will lead to ecological changes that are soon diluted by tributaries.



Lakes nested within river networks: patch dynamics and hierarchy

Spatial heterogeneity of habitat in streams occurs at multiple scales from grain size to entire catchments (Frissell et al. 1986). Poole (2002) elegantly showed how confluences within stream networks punctuate the river continuum resulting in abrupt changes in stream characteristics and nonlinearities in the expected gradient: a discontinuum network view. Later, Benda et al. (2004) provided a physical basis for predicting how confluences generate longitudinal spatial heterogeneity in habitat. The hierarchical patch dynamics view stresses variation in pattern rather than a continuum. In addition to confluences, there are many other sources of variation, including lakes, which are the focus of this paper. The RCC postulates a gradient in average conditions from the river headwater to lower-order reaches. Lake outlets, as described above, also generate predictable gradients in conditions but at a smaller scale, nested within the larger RCC gradient. In turn, lakes impose obvious spatial heterogeneity within the network that is precipitated downstream (cf. Pringle 1997).

Fig. 9. The position and size of lakes in a river network can have profound implications for the ecological characteristics of streams. The star represents a hypothetical sampling point in the network. (*a*) A relatively large lake in the headwaters of a network may significantly alter the characteristics of the stream. Further downstream, a lakeless tributary dilutes this lake effect. (*b*) A relatively small lake may have little influence on stream characteristics in the lower reaches of a network. (*c*) The combination of two lakes in the network influences the ecological characteristics of both main tributaries. (*d*) The position and size of lakes in a more realistic stream–lake network. The individual and combined influences of lakes on the network are complex and not easily summarized.



The influence that a lake has on the river is likely to decrease as the river grows larger down the network (Fig. 7). Lake size may increase with landscape position (Kratz et al. 1997); however, in some physiographic regions, large lakes are as likely to be located in headwater areas as lowlands. As river size increases, small lakes on its network path can become a river widening. In many cases, the distinction between a lake and a river is unclear. Functionally, a lake is perhaps defined by its ability to support lake forms of phytoplankton and zooplankton before entering the outlet where conditions are unfavourable for planktonic forms. The downstream distance of the lake effect increases as river size increases such that lake effects extend only metres in small streams to several kilometres in large rivers.

Drainage basin shape may determine the impact that lakes can have on a stream network. Dendritic networks, hierarchically branching and tree-like in form, typically develop in low-relief physiographic regions where relatively homogeneous geology exerts little control over development of drainage networks. Deranged and trellis networks, typical of the Canadian Shield (Fig. 8), are governed by geology and

Table 1. Potential measures and descriptors of stream–lake networks, including summary metrics of whole-watershed conditions, as well as a lake's potential to alter outlet stream characteristics.

Measure	Contributing measures	Rationale
Watershed-scale metrics of lake influence	Percentage of the watershed covered by lakes	High percentage, i.e., >10% of the watershed covered, may indicate a large lake influence on the system. The distribution, however, could be restricted to one large headwater lake.
	Position of lakes in watershed	Surface area or volume of lakes in headwater, midreaches, and lowland areas of watershed
	Percentage of river kilometres flowing through lakes or percentage flowing as river	A measure of overall lake effect
	Size distribution of lakes in the network	Many small lakes likely have less potential to alter streams.
	Cumulative lake-effect score for watershed	A measure of the influence of lakes on streams in the network
A lake's potential to alter downstream characteristics	Surface area or volume of lake relative to the size (width or discharge) of the inlet or outlet stream	Attributes of a small stream have the potential to be significantly altered when flowing into a large lake with a low flushing rate; in contrast, a larger river flowing in a small lake with a high flushing rate may retain many of its characteristics.
	Residence time	Mean time that water spends in a particular lake
	Sizes of inflowing streams	Bankfull width or stream discharge provide an indication of stream size.
	Highest order of stream flowing into lake	Provides an indication of stream size
	Flow path distance between inlet and outlet in lake	A lake with inlets and outlets at the opposite ends will alter the outlet stream attributes to the greatest degree, whereas inlets and outlets in close proximity may short-circuit the lake effect.
	Angle of inlet to outlet	The tributary angle of entry into the lake relative to outlet position
	Number of streams flowing into lake	A large number of streams flowing into a lake may indicate a short residence time.
	Basin shape	The ratio of basin area to the squared value of the basin length
	Distance downstream of a lake	Distance below the lake will determines the magnitude of the lake effect at a downstream sampling site. Coefficients and functional form of the downstream attenuation of lake effects is largely unknown.

can be densely populated with lakes, wetlands, and wandering interconnecting streams. Deranged and trellis networks are often long and rectangular (Briggs 1993), contrasting with round or teardrop-shaped dendritic drainages. A simple assessment of basin shape is the ratio of basin area to the squared value of the basin length. Calculated values of shape can range from near zero (elongated basins) to those approaching one (circular; Strahler 1968). These contrasting basin shapes illustrate how network configuration modifies lake effects. A single lake in the midreaches of a trellis network will alter ecological characteristics (e.g., flow regime) without the dilution from large neighbouring network branches for perhaps many kilometres (Fig. 8*a*). In the dendritic basin, the same placement of a lake will lead to ecological changes that are soon diluted by tributaries (Fig. 8*b*), which also create abrupt changes in the continuum (Benda et al. 2004).

Ecologists often build predictive models to understand how biological characteristics such as species presence or absence and diversity relate to landscape characteristics (e.g., McGarigal et al. 2002; Zorn and Wiley 2006). How well we quantify patterns in river networks will determine how well we can predict and understand their physical and biological attributes (Snelder et al. 2005; Seelbach et al. 2006; Brenden et al. 2008). Lakes connected to river networks present new challenges for deriving meaningful metrics of watersheds. In some cases, simple metrics such as the percentage of the watershed covered by lakes may be adequate to understand the relative influence of lakes on stream networks (Detenbeck et al. 2005). For more detailed metrics, the distance of a biological sampling point from upstream lakes of various sizes may be needed. For instance, what is the relative influence of a small lake 2 km upstream from a sampling point in comparison with a large lake 10 km upstream from a sampling point (Figs. 9*a*, 9*b*)? How does the influence of two or more lakes merge downstream to determine resultant stream condition (Figs. 9*c*, 9*d*)? Quantifying the attributes of stream–lake networks at the watershed-scale is challenging. The degree to which a lake can influence a stream might be estimated by considering lake size relative to the size of an inflowing stream, lake shape, and inlet and outlet position such that each lake in the network could be scored by its potential degree of alteration of stream properties from an otherwise lake-free network. Potential measures that could prove useful in describing stream–lake networks are summarized and postulated (Table 1). Clearly, much work needs to be done in this area to provide measures that are consistent with data availability and that may harmonize with other measures of stream networks and landscape position of lakes (Benda et al. 2004; Martin and Soranno 2006). Hopefully, complex landscape measures will emerge through future collabora-

tions between aquatic and landscape ecologists and the use of geographic information systems and remote-sensing data.

Further advances may be realized by incorporating landscape ecology and network analyses (e.g., graph theory) used in other disciplines such as epidemiology, studies of internet linkages, and transportation networks (Wiens 2002; Ganio et al. 2005; Proulx et al. 2005) to create a predictive science of biological networks. Graph theory provides existing techniques to examine the organization and function of biological systems, e.g., hierarchical branching stream–lake networks containing nodes (lakes and confluences) and edges (interconnecting streams), but has not attracted the attention of aquatic ecologists. Aside from providing a framework for understanding properties of stream–lake networks, other areas of scientific interest may benefit by applying network concepts to metapopulation and invasion ecology, connectivity (Schick and Lindley 2007), material and energy flow, and habitat heterogeneity in stream networks. Fresh ideas may emerge when we expand our view to the study of entire stream–lake networks, surpassing what we might learn from studying the parts (Proulx et al. 2005).

Lakes effects on fish communities in river networks

Piscivory by fish can be a dominant factor in structuring fish communities in both streams and lakes (Jackson et al. 2001). Lakes in stream networks can serve as a reservoir of predators and competitors, whereas streams can provide refuge from predators in the lake (e.g., lake trout (*Salvelinus namaycush*) and smallmouth bass (*Micropterus dolomieu*)). For example, Degerman and Sers (1994) found that the effect of lakes on water temperature, flow regime, drift of plankton, and invertebrates did not influence the stream fish fauna to the same extent as the presence of lentic fish (northern pike (*Esox lucius*); European perch (*Perca fluviatilis*); roach (*Rutilus rutilus*); and burbot (*Lota lota*)) in a zone upstream and downstream of the lakes. Correspondingly, the occurrences of stream fish (brown trout; European grayling (*Thymallus thymallus*); European minnow (*Phoxinus phoxinus*); and bullheads (*Cottus* spp.)) were lower close to lakes. The presence or absence of northern pike in lake networks in Sweden and Canada was a function of stream gradient (Jones et al. 2003*a*; Spens et al. 2007).

Lake inlet and outlet streams provide migratory pathways in a stream–lake network (Olden et al. 2001; Jones et al. 2003*c*; Daniels et al. 2008). This connectivity between lakes may provide colonization routes needed for metapopulations to persist, particularly in Arctic stream–lake networks where small streams and lakes typically freeze solid or in arid-region intermittent streams. Inlets and outlets may also provide critical habitat for spawning and rearing, whereas lakes provide overwintering habitat and refuge during drought (Dorava and Milner 2000; Luecke and MacKinnon 2008). Fishes in lake outlet systems may exhibit a simple adfluvial life history instead of a fluvial life history strategy consisting of distinct and lengthy migrations to spawning, feeding, and overwintering habitats (Northcote 1978; Jones et al. 2003*a*; Luecke and MacKinnon 2008). Based on the movements of fishes in Manitowish Chain of Lakes, Wisconsin, Weeks and Hansen (2009) suggested that walleye (*Sander vitreus*) be managed based on individual lakes and that muskellunge (*Esox masquinongy*) be managed for the entire lake chain. Overall, stream–lake networks provide a diverse array of habitats that may support a wider variety of species than would be present in lakeless steams. The mouths of lake inlets, and possibly outlets, can have relatively high biodiversity associated with different ecotones (Pinay et al. 1990; Willis and Magnuson 2000). Pringle (1997) notes that reservoirs and beavers dams can dramatically influence the spread of non-native fishes and source–sink dynamics in rivers. Although Pringle's focus was on perturbations downstream that have upstream impacts (e.g., dams, urbanization, water withdrawals), lakes on stream networks may have similar upstream consequences.

Challenges collaborations and questions

There are many unanswered questions about stream–lake networks that are fundamental to our understanding of fluvial ecology and our ability to design studies, interpret data, and manage natural resources. For example, what is the spatial and temporal variability of the lake effect and how far downstream is a significant lake effect observed? How does this vary with landscape position? Strong gradients in the physical, chemical, and biological characteristics of outlet streams have large implications for the design of ecological studies and impact assessments. Can lakes in a network "reset" the effects of natural and human disturbances? How do lake residence times, position, morphology, and size relative to stream discharge influence the characteristics of the outlet hydrograph? How important are lake outlet streams for providing migratory pathways and critical habitat (e.g., spawning, overwintering, and rearing) for fishes? And lastly, can the inhabitants of stream–lake networks show metapopulation dynamics?

Fruitful collaborations to resolve these questions will undoubtedly come from the combined efforts of limnologists, stream ecologists, and landscape ecologists. Geographic information systems will play an important role in summarizing landscape characteristics. Lake effects need to be more explicitly incorporated into ecological concepts in stream ecology, and limnologists would likely benefit by incorporating streams into their thinking. This comprehensive approach would help unify the study of aquatic ecosystems needed for the successful management and conservation of our aquatic resources.

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